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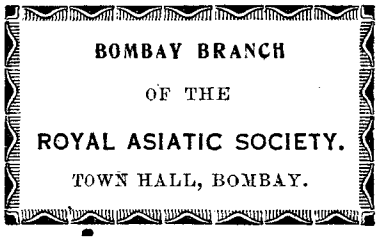

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ORGANOGRAPHY OF PLANTS

GOEBEL

HENRY FROWDE, M.A.

PUBLISHER TO THE UNIVERSITY OF OXFORD

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ORGANOGRAPHY OF PLANTS

ESPECIALLY OF THE

ARCHEGONIATAE AND SPERMAPHYTA

BY

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AUTHORIZED ENGLISH EDITION

BY

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PART I

GENERAL ORGANOGRAPHY

WITH 130 WOODCUTS

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PREFACE TO THE GERMAN EDITION

IF the botanical historian should ever write an account of that branch of the Botany of our times which is usually termed Morphology, he will probably look upon the period embraced within the last few years of the present century as one of transition. The conspicuous feature of transition-periods is the suppression of directive influences which have been dominant for a time because they are found to have served their purpose and lead no further. Newer views naturally conflict with the old and even with one another; things are found not to be so simple as was believed, and the old formularies cease to be applicable.

This change which has been in progress in Morphology is a consequence of the recognition by botanists that the configuration exhibited by plants is a part of their life-phenomena, and is not merely a hypothetical construction as it was made by the older idealistic Morphology. All the phenomena of life have a definite relationship to environment, and therefore, as I shall endeavour to show in this book, the consideration of the configuration of the organs of plants is not merely a comparative historical criticism, but must take into account all the conditions of environment which we find at the present day. Morphology has to determine in what degree the formation of organs shows an adaptation to external relationships, and to what extent it is dependent upon these and upon internal conditions; and even if the subject be studied from the purely phylogenetic standpoint, such determinations are a necessity, inasmuch as the historical development would be constantly influenced by environment. Phylogenetic speculations are doubtless more attractive than the grappling with the facts, often obscure and apparently insignificant, of the relationships of configuration of the plants around us. It appears to me, however, that to recognize the factors which bring about the development of say a leaf with one side larger than the other is infinitely more important than to construct a phylogenetic hypothesis unsupported by facts.

Hofmeister, Sachs, and Herbert Spencer have contributed in an especial degree during the later decades to the advancement of this modern line of study which we may designate Organography. It is yet in its infancy; a wide and little explored, yet promising field lies before us. The greatest difficulty I have found in preparing this work has been in stating the problems correctly in the part which is now issued dealing with the general aspect of the subject; and it is only after some hesitation that I have made the attempt. Although it does not claim to be an exhaustive treatment of the subject from every point of view, yet if it furnishes material for a subsequent treatise on general organography its appearance may be of use, and the more so, if it shows that the same problems are repeated in the most different cycles of affinity. This of course cannot be brought out so clearly in a special account of the different groups.

The object of the book may be best gathered from its contents. I may here only point out that it deals with the Archegoniatae and Spermaphyta alone; such mention as there is of the Thallophyta will be found in the general part, and there only for comparison with reference to these groups. I have not attempted completeness, and this is the case particularly in the statements of opinions different from my own; these are not referred to further than appeared to be necessary for the immediate purpose in view. The results of many investigations which have not yet been published have been made use of throughout this volume.

The authors—Strasburger, Noll, Schenk, Schimper—of the Textbook of Botany which has appeared through the same publishing-house as this book have granted the use of a number of figures; when these are original they are indicated by 'Lehrb.'

Dr. Arthur Weisse has prepared the account of the mechanical hypothesis of the position of leaves and he alone is responsible for the statements in it.

An index to the whole work will appear in the second part; in this first part an extended list of contents is given.

K. GOEBEL.

AMBACH,
September 1, 1897.

PREFATORY NOTE TO THE ENGLISH EDITION

THIS edition of Professor Goebel's interesting work brings within reach of English students the only book of recent years upon the subject of Organography of Plants, and is a valuable addition to the series of standard botanical books issued from the Oxford Press. Some of the interpretations and views to which Professor Goebel gives expression may not find unqualified acceptance, but the criticisms they will evoke and the experimental research which is sure to be stimulated by the Author's suggestive statement of problems requiring solution should further in no small degree the progress of our knowledge of the phenomena of life exhibited by plants.

The portion of the Special Part of the Book dealing with the Bryophyta, recently published in Germany, has been translated and will be issued along with a translation of the concluding portion of the volume when this has been completed by the Author.

Professor Goebel has himself read the English text and added a note.

My assistants, Mr. J. H. Burrage and Mr. H. F. Tagg, have been so kind as to undertake the labour of checking the references in the volume.

I. B. B.

EDINBURGH,
December, 1898.

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FIRST SECTION

GENERAL DIFFERENTIATION OF THE PLANT-BODY

GENERAL DIFFERENTIATION OF THE PLANT-BODY

I.

INTRODUCTION. MORPHOLOGY AND ORGANOGRAPHY.

THE botanical text-books of the day endeavour to arrange all that we know about plants in three sections—Morphology, Anatomy, and Physiology. The first two of these are sometimes combined as the morphology of the external and the internal members of plants. This however runs counter to the original signification of the word 'Morphology.' We owe the term morphology to Goethe. He says[1]: 'Scientific men in all time have striven to recognize living bodies as such, to understand the relations of their *external visible tangible* parts, and to interpret them as indications of what is within, and thereby in some measure to gain a comprehensive notion of the whole. . . . We find therefore in the march of art, of knowledge, and of science, many attempts to found and construct a doctrine which we may name the *morphology*.' It is quite evident then that morphology does not deal merely with the distinction and the naming of the outer parts of plants, although this, which really belongs to terminology, has been in part incorrectly called morphology. Morphology does demand the knowledge of the different appearances of the members of the plant-body, but only as a means to an end; it requires, not isolated facts, but the relation of facts to one another.

Terminology can be based on the study of dried plants, but morphology has, as Goethe stated, to do with 'living bodies,' which are

[1] Goethe, Bildung und Umbildung organischer Naturen.

involved in changes of a fixed character and are subjected to the influences exercised upon them by the outer world; it has, in other words, to do with that part of life-phenomena which finds expression in the external configuration.

The life-phenomena exhibited by plants are usually regarded as within the province of physiology, and the distinction which is drawn between physiology and morphology is, that physiology has to do with the *functions* of the organs of plants, whilst morphology takes no heed of these, but is rather a comparative and phylogenetic study. Sachs[1], for example, says: 'The parts of plants which we usually speak of as their organs, and which vary so much in form and serve such different physiological purposes, may be considered scientifically from two points of view. We may look at them as adapted by their form and structure for the carrying on of certain physiological processes, and in this case we regard them as agents for work—as organs. Such considerations are a part of physiology. On the other hand we may look at them apart altogether from these functions, and seek to determine where and how they arise, and in what relationships, both of space and time, the origin and the growth of one member[2] stand to those of another. This method falls within the province of morphology.'

A distinction of this kind is however, as Sachs expressly states, artificial and imperfect, and it may only be maintained so long as it does good service. As a matter of fact, it has finally led to one-sidedness, and its outcome has not infrequently been empty theorizing. In nature the form and function of an organ stand in the most intimate relation to each other; one is caused by the other. I take exactly the same view as is expressed by Herbert Spencer[3], whose work is far too little valued by botanists. He says: 'Everywhere structures in great measure determine functions; and everywhere functions are incessantly modifying structures. In nature, the two are inseparable co-operators; and science can give no true interpretation of nature, without keeping their co-operation constantly in view. An account of organic evolution, in its more special aspects, must be essentially an account of the inter-actions of structures and functions. . . .'

The title of the present volume is based upon the idea so aptly

---

[1] Sachs, Lehrb. der Botanik, ed. 4, p. 151. I cite this because it expresses clearly a conception that is even now widely prevalent. It is well known that Sachs himself changed his view. See for this his 'Lectures on Physiology,' and his 'Gesammelte Abhandlungen.'

[2] The word member (Glied) is the common term for an external organ (Organ) of plants and animals. There are no members which are not organs, leaving out of consideration of course cases of arrest. I am at a loss then to understand such a sentence as this: 'The morphology of plants knows no organs (Organe) but only members (Glieder) of the plant-body.' (Strasburger, Lehrb. ed. 2, p. 7.)

[3] Herbert Spencer, Principles of Biology, vol. ii. p. 4.

conveyed in these words, and the book which I wrote some sixteen years ago was likewise designedly entitled 'The Comparative History of Development of the *Organs* of Plants[1].' In the following pages the organs of plants are considered as being what they really are, organs or agents of work, but I have not gone into the *details* of their functions, I have only indicated in a general way the interdependence of form and function.

The first question to which we have to find an answer is: How came it that the functions of organs were entirely divorced from morphology? It is, and rightly so, one of the fundamental declarations of this study that the function of an organ tells nothing about its 'morphological significance,' or, in other words, the same function may be performed by organs of very different morphological value; 'homologous' organs must be distinguished from 'analogous' ones[2]. The tendrils of the vine and of the passion-flower, for example, are shoot-axes whose leaves are entirely or almost entirely suppressed; but the tendrils of the Leguminosae and of other plants, although like in form and function to those of the vine and passion-flower, are transformed leaves; the tendrils in the two cases are analogous, they are not homologous.

This knowledge is one of the weightiest acquisitions of morphology, but at the same time it has been the cause of an incorrect generalization. Because organs of like morphological significance may take on different functions, the functions which they perform have been considered as of subordinate importance, and therefore of no moment in the determination of the characters of the organs; hence it has been concluded that they must be entirely neglected in the grouping of the different members of plants in general categories.

This conclusion is erroneous, as will be briefly explained hereafter. If has led to an untenable position, especially in that fundamental problem of morphology which from the time of Goethe has been styled the 'Doctrine of Metamorphosis.' By this we understand the fact, that manifold as are the organs of plants, they can be referred back to a few 'fundamental forms' through whose 'transformation' the many and different members of the plant-body have arisen.

When we inquire how these primary forms and their transformations have been represented to us, we meet with different conceptions on the part of those authors who have taken pains to reflect upon the idea with which they dealt. In the idealistic morphology, as it was expounded by Goethe, A. Braun, and Hanstein, the doctrine of metamorphosis concerned itself

---

[1] Vergleichende Entwicklungsgeschichte der Pflanzenorgane, forming vol. iii. pt. 1 of Schenk's Handbuch der Botanik.

[2] See afterwards on pages 18, 19.

with an essentially theoretical construction, as I have elsewhere explained[1]. Goethe himself has plainly stated his view as follows: 'That which according to our *idea* is equal, may in reality appear either as equal or as similar, or indeed as completely unequal and dissimilar; this is the essence of the pliant life of nature.' In somewhat other form this idealistic notion has been preserved, inasmuch as the history of development was raised by the labours of K. F. Wolff, R. Brown, and Schleiden, to the rank of one of the most important aids to organography. The view which I have called the 'Differentiation theory' is based, as indeed is the whole of the doctrine of metamorphosis, on the study of the transformations of leaves, the manifold character of which is well known. Had its foundation been the transformation of the root instead of the leaf, the general notion of metamorphosis as merely a hypothetical transformation would have been replaced by the conception of it as an *actual transformation*—a view which, for many years, and in the face of active contradiction, I have endeavoured to establish. The differentiation theory assumes that at the vegetative point of the shoot *indifferent* primordia arise which are capable of development according to the needs of the plant in manifold ways, but have this in common—they are 'leaves'; the other view assumes a *real* transformation of a primordium in such a way, that, for example, the primordium of a foliage-leaf, instead of developing actually into a foliage-leaf, can become in the mature condition a leaf of quite a different character, a scale-leaf, say, or a sporophyll; similarly, the primordium of a stamen might become a petal. It will be seen that here a longer or shorter portion of the path of development is the same in the two primordia,—for instance, of a foliage-leaf and a scale-leaf. We speak of the scale-leaf as a transformation of the foliage-leaf, because in the juvenile condition we often find it to be possessed of parts which unfold themselves in the foliage-leaf, but become arrested in the scale-leaf; and further, we can experimentally hinder this transformation. The point is so clear in a case such as this that I will briefly illustrate it by an example[2]. Fig. 1 shows, at *I*, the outline of a foliage-leaf of Acer platanoides, and at *II*, the outline of a bud-scale. The two are outwardly very different structures. The foliage-leaf consists of the blade, *L*, of the stalk, *S*, and of the very small leaf-base, *G*; the bud-scale shows no differentiation, nevertheless it is nothing else but the transformed primordium of a foliage-leaf. If we examine more closely, and under some magnification, the small black tip of the bud-scale we find that it possesses a minute leaf-blade, or rather the rudiment of this,

[1] Vergleichende Entwicklungsgeschichte der Pflanzenorgane. Schenk's Handbuch der Botanik iii. 1. p. 103.

[2] See Goebel, Beitr. z. Morphologie und Physiologie des Blattes, in Botan. Zeitung, 1880, p. 753.

which has not developed further, but has died off. This interesting fact is explained when we follow the history of development of the foliage-leaf, which need only be looked at here in its coarsest features. At a certain stage of development of the foliage-leaf its form is something like what is shown at Fig. 1, *IV*. We recognize clearly the rudiment of the leaf-blade, *L*, and its lobes are already visible; the leaf-stalk has not yet appeared, but it will arise by the elongation of the zone lying between the leaf-blade, *L*, and the leaf-base, *G*. This stage of development is found in both foliage-leaf and bud-scale. But after this a change sets in: the primordium of the blade, *L*, dries up, the leaf-stalk is not developed, whilst the leaf-base grows considerably and itself forms the scale-leaf from which we started.

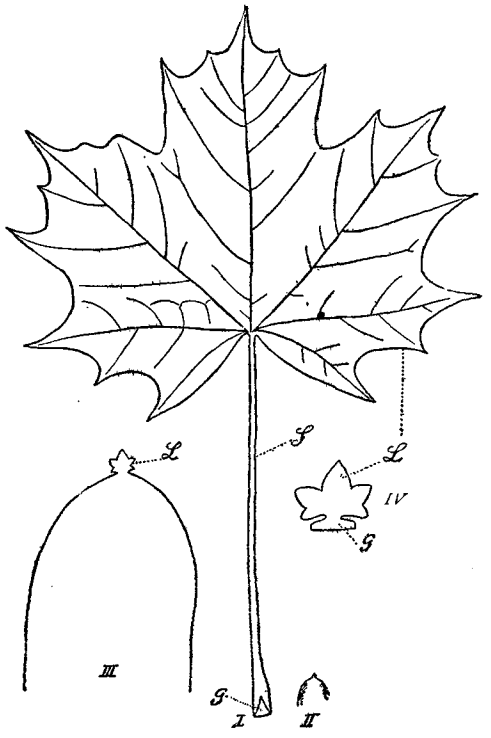

FIG. 1. Acer platanoides. *I* Foliage-leaf reduced; *G* leaf-base, *S* leaf-stalk. *II* Bud-scale. *III* Young bud-scale, magnified; *L* primordium of the leaf-blade which is arrested later. *IV* Primordium of foliage-leaf, enlarged and diagrammatic.

We are able, as I have already stated, to control experimentally the development of these leaf-primordia; one that would on account of its position develop normally as a scale-leaf we can force to become a foliage-leaf, and the converse is also true. It happens also, and this will be shown in the special part of this book, that the primordium of the blade may become arrested at a late stage of development. In Brownea erecta, for example, the buds are protected by erect dried-up foliage-leaves, the pinnules and other parts of which are clearly formed. It may frequently happen that the transformation takes place much earlier and is then of course no longer capable of *direct* proof, but only to be concluded upon comparative grounds. When now the differentiation theory says—the primordium of a scale-leaf and of a foliage-leaf of Acer are both 'leaf-primordia' which may sometimes develop in this way and sometimes in that, it entirely overlooks the point that the notion of 'leaf' is a purely abstract one, that

it is an artificially constructed category which has no concrete existence. What we see is foliage-leaves, scale-leaves, tendril-leaves, sporophylls, &c. That which these organs have *in common*, and which we endeavour to fix through a general idea, must be something else than their origin from 'leaf-primordia.' Seeing that if there are no leaves[1] there can be no primordia of leaves, either the primordia of foliage-leaves, scale-leaves, &c., are different from the outset, or they are alike for a time and then become different, and there must therefore be an actual transformation, a change in the course of development of *one* of these primordia out of which then the others can develop. That the primordia of the organs at the vegetative point are not of an indifferent nature, that they do not consist merely of embryonal tissue which is capable of development in any direction, is shown by the fact that the primordia of the leaves and of the lateral shoots are different from one another even at the moment when they appear as unmembered papillae upon the surface of the vegetative point. No case is known in which a papilla has developed into a shoot when its position indicated that it ought to be a primordium of a leaf, and the converse is also the case. And yet, as the remarkable example of Utricularia, which will be referred to in detail hereafter, shows, leaf and shoot are not categories of organs which are always sharply separated one from the other. We must therefore take it that primordium of shoot and primordium of leaf are usually different *from the beginning*, and in this we have confirmation of the conclusion already arrived at from simple analogy, that we must assume for the 'primordia of leaves' the possession from their outset of a definite, not an indifferent material nature which conditions their further development. This nature appears to be the same for all 'primordia of leaves' for a time[2]. Direct observation shows also that, as a matter of fact, a *modification* of the course of development frequently occurs, that a primordium upon which the several parts of a foliage-leaf can be already recognized may not become a foliage-leaf but something else. This modification of the development always stands in relation to a *change of function*. If the primordium of a foliage-leaf becomes a scale-leaf, it has of course never discharged the function of a foliage-leaf, but it had laid down the parts which are required for this function. This point may be illustrated even more clearly by cases in which *one and the same organ* shows a *change of function in successive periods* of its life. I will illustrate this by some examples:—

The basal foliage-leaves of Lilium candidum, and the similar leaves

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[1] For an instance of absolute misconception of this point and of the whole subject of transformation see the remarks of, amongst others, P. Vuillemins, in L'année biologique, i. (1895), p. 146.

[2] Compare the examples cited above.

in some species of Dielytra, at first perform the functions of ordinary foliage-leaves; after a time their lower part enlarges to form a scale-like tuber containing reserve-food, whilst the upper part dies off. The leaf has become *transformed*; it was first of all an organ of assimilation, later it has become in its lower part an organ of storage. Take again the case of the climber Quisqualis chinensis. The ordinary foliage-leaves perform the function normally attaching to them, but subsequently the lower part of the leaf-stalk changes its form, and becomes a hard woody hook, which acts as the climbing organ of the plant whilst the rest of the leaf is thrown off. In some species of Astragalus and Caragana the midribs of the pinnate leaves become thorns after the pinnules have fallen away. In these, as in many other cases, no one would deny that an actual transformation has taken place. An organ which was constructed for a definite function, and has performed this, takes on another function, and acquires another form.

Let us now assume, by way of example, that the leaf-pinnules in Astragalus fall away before they unfold, and before therefore they could act as assimilating organs, whilst the midrib develops into a thorn—would this not be a case of actual transformation? Of course it would; the change has only been advanced a stage. What we call the *mature* condition is only the terminal one of a series of stages of development which follow one on the other. These are however not independent of one another, but form a connected chain, one proceeding out of the other. If we designate a primordium of a 'leaf' at any one stage 'indifferent,' that means nothing more or less than a denial of the causal connexion of the developmental stages. A foliage-leaf does not become a foliage-leaf only in the last stages of its development; the material nature of the primordium, whether we look for this in the existence of a definite substance or of a definite structure, conditions the developmental progress. This consists of phases following one upon the other, the successive ones being always determined by those which precede them. Internal or external influences may however divert this development into other channels; thereupon a transformation takes place. The earlier this happens the less is it shown in the developmental history and the more different do the mature organs usually appear to be; but in the metamorphosis of the leaf, as I have already shown, every degree of gradation is found, and this furnishes the explanation of the frequent appearance of formations possessing characters intermediate between two organs. These intermediate stages are very common in the case of 'abnormal' transformations, which will be treated of in the Fourth Section of this book, but they are also frequent as normal occurrences, in the case of bud-scales, for example, as well as in other cases which are easy to observe, and of which I shall here mention a few.

The inflorescences of Nidularium splendens, one of the Bromeliaceae, are surrounded by a number of beautiful red 'bract-leaves,' which differ from one another, and which make a showy attraction-apparatus. The lowermost are quite like the ordinary foliage-leaves, except that their basal part is red. In succeeding leaves the red portion gradually increases until, in the uppermost, the *entire* leaf from base to apex is so coloured. We may state this otherwise by saying that the transformation, which here appears in the red colouration, commences sometimes earlier, sometimes later, in the development of the primordium of the foliage-leaf. The basal portion is that which matures latest in the development of a leaf, and consequently when the transformation commences relatively late the basal portion *only* is affected, the other parts are normal[1]. In other Bromeliaceae, as, for example, Bilbergia, the passage from foliage-leaves to bract-leaves is abrupt, yet the transformation itself remains the same. Similar examples may be found in many plants producing tendrils. In such tendrillous Fumariaceae as Corydalis claviculata we find in the successive leaves of the seedling all transitions from ordinary foliage-leaves which have not tendrils to those with tendrils; the stalks of the upper leaflets gradually elongate whilst their blades correspondingly diminish until typical flagelliform tendrils are produced. In Cobaea scandens, a tendrillous plant of the Polemoniaceae, the transition from leaves without tendrils to leaves with tendrils is on the other hand a sudden one; but the developmental history of the tendrils here shows[2] that they arise in quite the same way as is so easily observable in the seedling plant of Corydalis claviculata—the tendrils themselves are greatly elongated leaf-petioles gifted with a special sensitiveness, and the blades of the leaflets are visible as small papillae at their terminations. We do not however find in all tendrils the transformation of the primordium of the foliage-leaf taking the course we have described. The *whole* leaf-primordium may be concerned in the formation of the flagelliform tendril. The history of development of the first tendrils of Benincasa cerifera, one of the Cucurbitaceae, for example, shows us that a leaf-blade is distinctly laid down upon them, but the whole leaf instead of developing into a flat expansion elongates into a long filiform tendril; this is not the case in subsequent leaves. Numerous other examples will be given in the special part of this book.

One of the weightiest facts of the organography of plants is, in my opinion, the indication that there is a traceable and direct developmental

[1] Eranthemum nervosum, a plant often cultivated in Botanic Gardens, shows a like condition of the bract-leaves.

[2] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, p. 431. Compare also A. Mann, 'Was bedeutet Metamorphose in der Botanik?' Inaug. Dissertation. Munich, 1894.

history in the formation of organs. There are many experimental proofs of this furnished partly by nature itself, partly through artificial methods, of which some mention must now be made. If the flower-buds of Knautia arvensis are attacked by the fungus Peronospora violacea, the staminal primordia commonly develop into petals. These primordia were not however 'indifferent.' The series of processes through which they would become stamens had already begun when the attack of the fungus turned the development in another direction. Other similar examples will be found in the section upon malformations; I will only mention here that, as my investigations have proved, a simple disturbance may hinder the transformation of the primordia of foliage-leaves into scale-leaves, and, as the case of Onoclea Struthiopteris shows, a transformation to sporophylls may be likewise prevented[1]. To this instance I may refer further here. The sporangia of ferns arise on leaves which are termed sporophylls. These are either quite like the foliage-leaves, as is the case in Aspidium Filix-mas, or the formation of sporangia causes more or less profound changes in the form, direction, and structure, of the sporophyll. Onoclea Struthiopteris belongs to that group of ferns in which such differences are the greatest; and its sporophylls are produced in regular alternation with the foliage-leaves. For a considerable time their development conforms with that of the primordia of the foliage-leaves, it is only when the formation of sporangia sets in that a modification in its course is observed. If now all the foliage-leaves be removed from the plant the development of sporophylls is hindered; the primordia of the sporophylls, which are nothing else than primordia of foliage-leaves, are then forced to develop into foliage-leaves and the production of sporangia is either partially or entirely suppressed. From the point of view also of inheritance, by which we mean the repetition in descendants of their ancestral development apart from small deviations, it is of importance that only definite organ-primordia need to be transmitted, and out of their transformation others then proceed; only the causes of such transformation are not, as in the example of Knautia above referred to, external, but internal—they belong to the capacity of the plant itself.

Our idea of metamorphosis is then primarily an ontogenetic one and is therefore capable of experimental measurement and proof. Phylogenetic considerations may come in, but the incorrectness of speaking of a metamorphosis purely in a phylogenetic sense is shown by this simple fact that the doctrine of metamorphosis is older than the theory of descent, and would remain even if the latter were given up.

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[1] Goebel, Über künstliche Vergrünung der Sporophylle von Onoclea Struthiopteris, Hoffm., in Ber. d. deutschen botan. Gesellsch. Bd. v (1887), p. lxix.

We limit therefore the idea of transformation to cases where the change of function is evident. The *foliage-leaves* in one and the same plant frequently differ from one another in configuration, but where no other functions than those of assimilation and transpiration appear prominent it is better not to speak of a transformation but only of a different construction. As is the case in all attempts to set artificial boundaries in matters relating to living organisms, it is impossible here to draw sharply defined limits, and especially between the small deviations in function which always go hand in hand with differences in configuration. In the root-system of a dicotyledonous plant, for example, the chief root and lateral roots are organs which have essentially the same function and configuration, and yet there are differences between the two of physiological behaviour and of construction—differences in which we may recognize at one time phenomena of correlation, and at another dissimilarity in reaction towards external influences. That a lateral rootlet owes the differences which mark it from the chief root only to its position in the root-system is apparent, inasmuch as it can be readily caused to develop as a chief root. The differences between chief root and lateral root are then too slight to allow of our speaking of a 'metamorphosis.'

I have said above that if the doctrine of metamorphosis had been developed upon the facts observed in the roots instead of the leaves it would not have led to such illogical conceptions as has been the case. When one speaks of a 'root' in one of the higher plants one does not think of it as an abstract idea but as quite a definite object—a leafless cylindric organ provided with a root-cap. This is so because in the root change of function is a much more rare occurrence than it is in the 'leaf,' and consequently it has not happened that the idea of the root has been gradually generalized so as to leave only an abstraction with which nothing can be identified. There are however not a few cases in which roots are transformed, and these we can easily follow. For example, we see that the root when it is transformed into a shoot throws off its root-cap, as in Platycerium and some other ferns, as well as in some Spermaphyta; and the same thing happens, along with the necessary change in the tissues, when the root becomes a thorn, as it does in Myrmecodia echinata and Acanthorhiza aculeata, or forms a tuber to serve as a reservoir of food. In the case of the root also, the change of function may set in *before* the root has exercised its original function of a nourishing and anchoring organ.

The result of what has preceded is then as follows:—The idea that morphology has nothing to do with the function of organs has been acquired entirely because the fact has been overlooked that the transformations seen in organs are conditioned by a *change of function*. Their functions therefore have been treated as subordinate in determining

the characters of organs; external relations alone have been taken as the chief points for consideration. But the relationships of mere form are by no means the permanent ones in 'the tide of phenomena.' They also change. The determination of this change, that is to say, of the alterations which have taken place and are believed to take place in the formation of organs of a natural group, is one of the weightiest tasks of organography. If we separate function from form we are at once led into altogether unfruitful speculations. Further proofs of this will be given in the following pages.

II.

DIFFERENTIATION OF ORGANS IN THE SPERMAPHYTA.

The higher plants, as the forms of vegetation which were earliest studied, naturally supplied the material for the first identification and terminology of the organs of plants. When the 'Doctrine of Metamorphosis' established the conception that the many and varied organs possessed by these plants were all referable to but a few 'primary forms,' the definition and limitation of these became a necessity. Hence arose a morphology based upon the consideration of the form of the vegetative organs alone, which, while it could determine the sporophyll of the flower to be simply a 'leaf'-organ, could not recognize the significance of the sporangium; this was only possible by comparison with the Pteridophyta.

The outcome of early and simple observations was the recognition of root, stem, and leaf (foliage-leaf) as the chief *vegetative* organs of the higher plants. To these organs was added subsequently the hair, a structure springing from the epidermal cells and appearing as an appendage of the surface. When it was found that in the construction of many prickles and glands layers of the tissue deeper than the epidermis were involved, the term 'emergence' was coined for them—a term, the definition of which is framed upon essentially negative characters: emergences are neither leaves, nor shoots, nor roots, and are not endogenetic. Afterwards when the stem, the leaf, and the hair, were considered as abstractions, and apart from all their varying special forms, they received the designation respectively of caulome, phyllome, and trichome. Although morphology has never yet succeeded in framing generally applicable definitions to distinguish these categories of organs from one another, there are never-

theless but few cases where any doubt exists as to the category to which a definite organ belongs, in other words, its morphological significance or 'homology' is clear. This notion of homology I must now discuss.

Just as in systematic botany no *single character* can be considered as a critical mark of affinity, so also no single mark can be taken as a criterion of the homology of an organ, but it is groups of peculiarities which are of morphological value and give us the key to homology. What has to be determined is the position of an organ in the whole development, to what organ of an allied form it corresponds, through what transformations it has passed, that is to say, what *change of function* has befallen it. We shall see hereafter to what unprofitable speculations the neglect of these principles has led, especially in the consideration of the organs of propagation. It is these organs which occasion one of the greatest of the difficulties which arise in the way of the definition of the *vegetative* organs. The special organs of propagation—sporangia, oogonia, and the like—exhibit in the nature of their case no change in their function; their function and form are fixed, and this is what gives them their chief value in systematic work.

It will be useful if I refer here to the endeavours which have been made to fix the limitations of organs of plants, because the question itself is of importance and much uncertainty even now prevails regarding it[1].

1. It is manifest that the distinction of organs must have originally been based upon differences of outer form. The word 'blade' indicates that the original conception of a leaf was that of a flat organ which was distinguished by this character from the usually cylindric stem; under the designation root, all subterranean organs were reckoned. It is however now generally known that there are leaves which have all the appearance of shoots, and the converse is also the case. Nevertheless, in one of the most recent text-books the leaves of the rush are designated leafless 'shoot-axes' because they have the appearance of cylindric leafless shoots, and in the same work the rhizoids of the moss are termed 'hairs' only because they have the appearance of the hairs of higher plants, and although they have otherwise nothing whatever to do with them.

2. External form is closely connected with function and with anatomical structure. In the vegetative organs the form may change, accompanied by a change in anatomical structure; 'metamorphosis' may take place, and a flower-leaf is the homologue of a foliage-leaf notwithstanding that it has quite a different form. The anatomical structure of homologous organs is often very different, and the attempts which have been made to prove upon anatomical grounds the leaf-like twigs of

[1] Consult Goebel, Vergleichende Entwicklungsgeschichte, p. 127; Bower, On the limits of the use of the terms 'Phyllome' and 'Caulome,' in Annals of Botany, i. p. 133.

Ruscus and other plants to be leaves are so futile as to be hardly worth rescuing from their deserved oblivion.

3. The history of development of the stem and of the leaf is usually different. In the first place the duration of development is unlike; leaves have limited growth, shoots have unlimited growth. But there are many shoots which normally exhibit limited growth, for example, the short shoots or spur-shoots of many conifers and broad-leaved trees; these however may under certain conditions become shoots of unlimited growth and be transformed into long shoots. There is no real specific difference between spur-shoots and long shoots, the limitation of their developmental capacity is determined only by their position on the tree. We do not know however that this is true of all spur-shoots. It is probable, for example, that the needle-like leafless assimilating short shoots of Asparagus were from the first laid down as shoots of limited development, and that therefore the same reduction in the formation of the organ took place here as we often meet with. Similar features appear in the lower plants. Thus the 'leaves' of Chara are merely short shoots, but it is impossible, so far as we at present know, to cause them to develop into long shoots, and it is extremely improbable that this will take place. Again, no one has succeeded in forcing artificially a leaf of one of the Spermaphyta to unlimited development. Nature however sometimes tries this experiment. The leaves of some ferns continue to grow at their points in successive periods of vegetation. But a much more striking illustration is furnished by species of the genus Utricularia, which are amongst the most remarkable plants in the world. In this genus the floating 'shoots' of the water-form, as well as the creeping 'stolons' of the land-form, are, as I have proved [1], homologous with leaves; but the difference between stem and leaf has entirely disappeared. The organs which are homologous with leaves produce flowers and other shoots, and exhibit unlimited growth; and that they are really leaves with prolonged apical growth is only to be determined by a careful comparative study. Every distinction then that we may draw between shoot and leaf is only relative, is not fundamental. The method in which the leaves are laid down at the vegetative point of the shoot-axes is not fundamentally different from that exhibited by the shoots, and no advantage would be gained by discussing here the question of the degree in which the several cell-layers of a vegetative point share in the primordium of leaf or of shoot. There is however this point still to notice—leaves are in most cases outgrowths of shoot-axes, and they arise on their vegetative point as lateral members; nevertheless terminal

[1] Goebel, Der Aufbau von Utricularia, in Flora, 1889, p. 291. More details will be found in Morph. u. biolog. Studien, in Ann. du Jardin Botanique de Buitenzorg, vol. ix. p. 2.

leaf-organs—organs arising from the end of a shoot-axis—are known. They occur in the flowers of many plants, as we shall see later; the cotyledon in many monocotyledonous plants is terminal in the embryo; there are also monocotyledonous embryos upon which leaves arise although no vegetative point of the axis is visible, and a similar condition is also found in Isoetes; further, the vegetative body of Lemna is nothing else than a leaf producing leaves[1], it is not a leafless twig[2] as is commonly assumed.

All attempts that have been made to give a simple definition of 'caulome' and of 'phyllome' have failed, and this is not surprising seeing that none of the characters upon which they have been based are constant in all of the different cycles of affinity. Plants, it must be remembered, are living things, and the formation of their organs cannot be circumscribed by definitions. What we can say, and what indeed is alone of interest, is this—the modifications which the formation of the organs undergo in any one group can only be determined by comparing *all* their characters. We have no data enabling us to determine the phylogenetic history of the leaves of the Spermaphyta, and therefore a fictitious interest only attaches to speculations upon the subject. We shall see hereafter that the part of the plant-body which, with Sachs, we designedly term *shoot*, has become differentiated into stem and leaf, often in the most different ways in different groups of the plant-kingdom.

The hair supplies us with a striking illustration of how misleading it is to endeavour to find diagnostic marks of an organ in *one* character. Hairs or trichomes are structures which are found upon the epidermis of plants. It is doubtful in the case of ordinary typical hairs whether there is any *advantage* in combining under one name organs which, whilst they share with one another so superficial a character, are yet fitted for the performance of the most different functions. There would be some sound foundation for the terminology if these organs stood in any intimate genetic relationship with each other; if, for example, it could be proved that the gland-hairs of the Labiatae are the homologues of the woolly hairs which are found in so many species of the family, and that these two hair-forms were derived from a common ancestral form or could be transformed one into the other[3]. Such a connexion may be established in many hair-forms, but it certainly does *not* exist in very many others, and the majority of different hair-forms have their epidermal origin *only* as a common character, and this is but a superficial one. If I were to find in an intercellular space within one

[1] See my 'Pflanzenbiologische Schilderungen,' ii. p. 274.

[2] Hofmeister described the leaves of Pistia as leafless twigs.

[3] I have no doubt that hairs do change their function. In a recent paper I have shown that the water-secreting hairs of Rhinantheae arise from gland-hairs. See Flora, 1897, p. 444.

of the Labiatae a 'gland-hair' possessing the same structure and the same peculiar features as one growing from the epidermis I would certainly call it a 'gland-hair.' The position and origin of an organ is in my view *one* point of importance, but it is not the only criterion by which to judge. Every single organ is built up through a series of regular succeeding developmental stages which are based on its material nature and which can be changed in certain ways. Why should the change not produce its effect at the place of origin of the organ? The antheridia of most liverworts arise from surface-cells, but those of Anthoceros occur in a closed depression. Are we then to regard the antheridia of Anthoceros as not homologous with those of the other liverworts? The question we have to answer here is only—how have the antheridia of Anthoceros got into the pit, and has this deviation any special significance for them? The point is not—does their position make them different from the other antheridia of the liverworts? In speaking of the organs of vegetation there is no doubt that the use of the expression 'trichome,' based upon the seat of origin of an organ, is in many cases very convenient, but it is absurd to call many reproductive organs of plants 'trichomes,' as is so often still done, simply because they arise upon the epidermis. The reasons against it which I have previously established have in great measure been overlooked, and I will therefore repeat them here.

Origin of an organ from the epidermis is one aspect, but only *one*, and that a purely technical one, of the development. What we have to learn is not only *how an organ arises*, but before everything else, *what it is*, and if we venture upon the statement that all 'trichomes' arise from the epidermis the converse is very apt to be assumed that everything that arises out of the epidermis is a trichome. Leaf-structures also sometimes arise from the outermost cell-layer of the vegetative point, as Strasburger has shown to be the case with the perianth of Ephedra, and the adventitious shoots which develop upon detached leaves of Begonia arise commonly, according to Hansen, from a single epidermal cell. No intelligent man would on this account call them trichomes. There is as little sense, to my thinking, in calling the sporangia of ferns 'trichomes' as is so often done, because neither in ontogeny nor in phylogeny is there any evidence that a sporangium has been derived from a hair through a change of its function. Although we cannot trace the phylogenetic development of the Pteridophyta we know that the sporiferous generation is the homologue of the sporogonium of a moss; but by what process of development the sporangia have been differentiated from a sporogonium-like structure we can only conjecture. If we had a record of this history we should know the 'morphological value' of the sporangium; for us nowadays to refer it to a hair-structure is simple nonsense; in many cases the hairs had probably an origin much subsequent to that of the sporangium.

We might say very much the same about other organs of propagation, such, for example, as the nucellus of the ovule, and the antheridia and the archegonia of the Archegoniatae. The antheridia of mosses are formed, as is well known, sometimes as terminations of the apex of the stem, sometimes in the position of leaves or hairs. What this teaches us is that the place of origin varies, and if, looking at the fact, we say that the 'morphological significance' of the antheridium varies, we can only mean that the morphological significance is in this sense of subordinate importance. The organs of propagation naturally arise on preceding vegetative organs, and the vegetative organs which produce the propagative organs are frequently transformed in a characteristic manner. But the propagative organs cannot be referred back to vegetative organs. Looked at from the phylogenetic point of view they have been in existence, although in a simpler form, *before* the vegetative body reached the differentiation it now possesses. Amongst the Spermaphyta in particular the structures bearing the propagative organs have not been sufficiently distinguished from the vegetative organs. A stamen, for example, is considered an individual structure, and yet it consists of a sporophyll and a sporangium (pollen-sac), which is often sunk in it. The sporophyll is a transformed leaf[1]; and with regard to the sporangium, while it is absurd to view it as a transformed part of a leaf, it is a weighty accession to our knowledge to determine it to be the homologue of the sporangium in the Pteridophyta. The expression 'homologue' may be here further explained, for it is used in different senses which can be well illustrated by consideration of the stamens. When I say—a stamen is the homologue of a leaf, the pollen-sac is the homologue of a sporangium, or, if you will, of a row of sporangia—the term has not the same signification in the two cases. A pollen-sac is a sporangium because of its *function* inasmuch as it produces spores, and it occupies in the whole plant-economy of one of the Spermaphyta the position which a microsporangium holds in that of a Selaginella. A stamen is a *transformed* leaf which has acquired another form and function because it produces sporangia. Had all the Pteridophyta, especially the heterosporous ones, been destroyed, we should not have been able to determine the correspondence of the pollen-sac with the sporangium; on the other hand, were the earth covered with Spermaphyta alone, we should be able to ascertain that a stamen is a transformed leaf. It is necessary to distinguish these two points of view. Homologous organs are commonly defined as those for which we can trace a common phylogenetic origin, far back although this sometimes goes. But careful investigation cannot fail to convince us that many *different* lines of development have

[1] For a discussion of opposite views, especially that of Bower, see Part II of this book.

frequently proceeded from very simple forms as their starting point, and yet that the formation of organs has taken place along these lines in a more or less similar manner because of the similar *capacity* for development they have derived from the 'stem form'; in other words, the material nature being similar the development must proceed along a similar path. As an example of this we may cite the homologous sporogonia of the mosses and liverworts. In them we have two series which must have branched off the one from the other when the formation of sporangia was as simple as we find it nowadays in Coleochaete [1], where indeed we can scarcely speak of sporangia. In both series the further development has gone to a considerable length, but whilst the essentials of the sporangia, which lie only in the function of producing spores, have been retained in both, the relationships of configuration otherwise have diverged in widely different directions.

The vegetative organs of the liverworts furnish even a better illustration of this. If we assume that there has been a main line of development it must have happened that the leafy shoots of the liverworts have taken origin *more than once as different series* independent of one another. The leaves of the acrogynous and anacrogynous liverworts, which we may take as an example, would then not be homologous; nevertheless they arise on the vegetative apex in essentially the same way, and conform so closely with one another in their other features that they are clearly structures which have something in common. It often happens that with such examples before us we speak of a homology of organization which is really not phylogenetic, or at least has only to do with phylogeny in so far as it recognizes a common capacity for development derivable from undifferentiated ancestors. Such a conception is a more complex one than that involved in the ordinary and usually somewhat speculative phylogenetic definitions, but it fits the facts better.

Analogous structures, by which we mean organs which are alike only in their 'adaptation' to the outer world, and this, it must be remembered, may be achieved in quite different ways, should be distinguished from those which are homologous. I need only here recall, in illustration, the occurrence of Euphorbiaceae with the habit of Cacteae; the many plants possessing needle-leaves and belonging to different families; the occurrence of a porose capsule in Polytrichum as well as in Papaver; the appearance of elaters quite similar to those of many liverworts in Battarea, one of the Fungi. It is facts like these which have led to the belief that morphology has no concern with the function of organs, because otherwise homologous and analogous organs might be confused; but we have

[1] I do not regard Coleochaete as an 'archetype' of the Archegoniatae, and I mention it here merely for the sake of a comparison.

seen that this belief is erroneous, and that, bearing in mind the fact that frequent change of function has taken place, we require [1] to read function into the characters through which we diagnose organs.

In the light of what I have said we may distinguish in the higher plants [2] :—

(1) Vegetative organs, namely, root and shoot, with their appendages, which may be grouped as hairs or emergences.

(2) Propagative organs, namely, sporangia (including sporogonia), and the sexual organs—antheridia, and oogonia or archegonia.

In the higher plants the shoot is differentiated into shoot-axis and leaf in all cases except in some degenerate parasites. There are, it is true, leafless shoots of limited growth, for example, the needle-like or leaf-like assimilation-shoots in species of Asparagus, the bristles of the inflorescence of Setaria and Cenchrus, but these are quite exceptions. It is remarkable that in the most different cycles of affinity of plants in which the leaves have been arrested a differentiation nevertheless takes place, which exhibits clearly and without the necessity of careful morphological investigation the construction characteristic of a leafy plant. The 'phylloclades' of many monocotyledonous plants are the best known examples of this, but we find similar features in species of Phyllanthus and in a number of succulent plants both of the Cacteae and the Euphorbiaceae [3]. In the lower forms of plant-life such a differentiation of the shoot may also take place. The sexual generation of many liverworts and of the whole of the mosses shows an evident division into shoot-axis and leaf, and, as has been above explained, this condition is reached amongst the liverworts in the most different cycles of affinity, which have developed quite independently one of the other. That the leaves of the sexual generation of mosses are not homologous with those of the asexual generation of the Pteridophyta is sufficiently clear. Are we then to use different names for them? Such a proposal has already been made by Bower [4]. But is there any advantage in this? In my opinion it is simpler to retain the old designation with the caution that it is based upon analogy not upon homology. The more complex the technical terminology is in a science, the more difficult it is to handle, and we must remember that after all terminology is only a means to an end [5]. I have therefore

[1] How could a flower or a stamen be defined without reference to its function?

[2] Pteridophyta and Spermaphyta.

[3] See my 'Pflanzenbiologische Schilderungen,' I., for figures.

[4] Bower, On the limits of the use of the terms 'Phyllome' and 'Caulome,' in Annals of Botany, i. p. 135.

[5] It is different when consideration of the homology induces us to put aside unnecessary terms. The term 'corpuscle' for the archegonium of Gymnospermae is now fallen quite out of use, and when we use the term 'microsporangium' for the pollen-sac, this is not the introduction of a new term but only the transferring to the Spermaphyta of a term which is in common use when speaking of the Pteridophyta.

no hesitation in calling the leaf-like organs which we find in many Thallophyta 'leaves.' Some Florideae have throughout a differentiation analogous with what is found in the higher plants, for example, Polyzonia jungermannioides which is represented in Fig. 17; examples too are not wanting in different developmental series of the Phaeophyceae, such as the Laminariaceae and Fucaceae.

The way in which this differentiation into shoot-axis and leaf has come about varies considerably. It will be briefly shown in the next chapter how in the lower plants such a differentiation has been reached by different paths from quite simple beginnings.

III.

FORMATION OF ORGANS AND DIVISION OF LABOUR AMONGST THE LOWER PLANTS (THALLOPHYTA).

A plant-body in which the shoot-axis does not exhibit differentiation into stem and leaf is termed a *thallus*. The earlier writers called the thallus a 'frond' when it was flat and leaf-like, but this is a superfluous term which has fortunately dropped out of use. The expression thallus, which signifies nothing more than shoot, was first used by Acharius[1] in describing the lichens, and subsequently it was extended to the Algae, the Fungi, and the thallose liverworts. There is no sharp limitation between a thallus and a leafy shoot as the examples which will be presently noted clearly show. Endeavours have also been made to establish the idea of the 'phytome' in addition to that of the thallus. By this term Naegeli designated the plant-body of unicellular plants, and of such as consist of entirely *similar* cells whether unbranched or branched, provided that in the latter case the branches be always similar to one another and to the mother-organ. The distinction between the phytome and the thallus was based on the fact that the thallus could produce 'trichomes.' The distinction is altogether superfluous. The idea underlying the expression many-celled 'phytome' is included in that of *colonies* or *coenobia*, which will be described presently, and it is impossible to speak of 'trichomes' among the Thallophyta in the same sense as we speak of them amongst the higher plants. The organs which have

[1] Acharius, Lichenographia universalis. Gottingae, 1810, p. 3—'In omni Licheno completo duae . . . sese offerunt partes, quarum una corpus ipsius Lichenis constituens thallus a me dicitur . . .'

been called hair-like among the Thallophyta have the most different origin and the most different functions[1]—they may be fixing organs, they may be protective organs of the most various kinds, for example, secreters of mucilage, and there are many the exact significance of which we do not know. They have this only in common, that they appear as small appendages of the thallus and have often a certain external resemblance to the hairs of higher plants, but, as there is no epidermis here, they want naturally the technical character which belongs to hairs of higher plants and which, as we have seen above, is regarded as critical.

The lower plants furnish a starting-point for the determination of the critical marks of organs, inasmuch as they exhibit a series of gradual differentiations of organs in relation to division of labour in their functions, and they do this not only along one line but they repeat it in several different series. The differentiations of members which we find in the higher plants are therefore to be considered as merely special cases of these more general ones.

UNICELLULAR AND PLURICELLULAR PLANTS, CELL-COLONIES AND CELL-DOMINIONS[2].

The external relationships of configuration of the bodies of plants are determined by the peculiarities of their living substance, the protoplasm, which in the higher plants is enclosed within the numerous cells which compose the plant; it is only amongst the lower plants that we find unicellular bodies. Sachs[3] has however shown that the traditional idea of the cell is now become inapt and that it leads often to incorrect comparisons. If we speak of a caulerpa and a diatom or desmid as unicellular we only indicate thereby *one* external circumstance, namely, that these plants consist of a non-chambered protoplasm invested by a cell-wall[4]. But the inner structure of the protoplasm is very different in the cases cited, and the difference is marked by the presence in the diatom and

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[1] See, amongst others, Moebius, Morphologie der haarartigen Organe bei den Algen, in Biolog. Centralblatt, xii. p. 71.

[2] [The word *dominion* is used to convey the meaning of the German 'Staat.' To have employed the literal translation 'cell-state' as the equivalent of the German 'Zellstaat' might have led to confusion for obvious reasons.]

[3] See especially his Physiologische Notizen: II. Beiträge zur Zellentheorie, in Flora, lxxv (1892), p. 57; and IX. Weitere Betrachtungen über Energiden und Zellen, in Flora, lxxxi (Ergbd. z. Jahrg. 1895).

[4] L. Klein says, for example: 'The highest stage of construction reached by an unicellular individual is found in the Siphonieae . . ; in which nature shows to what height of development it is possible for a single cell to attain, for this is the character of the thallus in these plants notwithstanding the great amount of division of labour it exhibits.' Unters. über Morphologie und Biologie der Fortpflanzung bei der Gattung Volvox, in Ber. d. Naturf.-Ges. zu Freiburg i. B., v (1890), p. 43.

desmid of only one cell-nucleus, whilst in the caulerpa there are many nuclei. This clearly indicates a difference in degree of organization which may be illustrated as follows:—Let us suppose *A* to be a cell with one nucleus and *B* to be a cell with many nuclei. Both may multiply by swarm-spores. In *B* this may take place simply by each of the cell-nuclei becoming surrounded with protoplasm, and the protoplasmic body in this instance breaks up into isolated parts. In *A*, on the other hand, a repeated series of divisions must take place before the same result is reached. The plurinucleate cell is then in point of time ahead of the uninucleate one in differentiation, and shows in the possession of many nuclei a feature in its vegetative life that only appears in the uninucleate cell at the time of propagation. The plurinucleate plant-body does not correspond with the vegetative stage of the uninucleate cell, but with that which this cell reaches just before propagation. These reflexions lead us to Sachs' notion of energids. 'By an energid,' says Sachs, 'I mean a single nucleus with the protoplasm it dominates.' These energids may be enclosed singly or a number of them together in a cell-chamber. It is not necessary that the mass of protoplasm 'dominated' by a cell-nucleus should be always the same[1], but the behaviour of the nuclei in the formation of the propagative organs of Siphonieae indicates plainly the important influence the 'energids' exercise in the process; and similar evidence is forthcoming from regeneration. Into all processes of propagation which have been accurately investigated, whether these be sexual or asexual, either single energids enter or, where this is not the case, as happens with the swarm-spores in Vaucheria[2], the cilia indicate that we have to deal with a body which is not a simple one but is composed of many energids. Our recently acquired knowledge of the cell teaches us then that we must no longer distinguish between unicellular and pluricellular but between monergic and polyergic plants[3]. Polyergic plants may be divided into cellular, which is the usual form, and non-cellular groups, according as the energids are enclosed or are not enclosed in chambers. Examples of polyergic non-cellular plants are the Myxomycetes, if one reckons these as plants, and the Siphonieae, which have only an external circumscribing membrane. Both these groups, it will be noticed, are composed of organisms which are aquatic or dwell in moist spots—the Myxomycetes living concealed in these moist places until

[1] Rider and horse in a cavalry regiment form a 'unit' even although the horse be changed.

[2] Schmitz has proved that there are two cilia to each cell-nucleus, or as we now say to each energid, and the whole pluriciliate swarm-spore is therefore composed of numerous biciliate ones. The difference between monergic and polyergic cells shows itself specially in their behaviour in regeneration.' In this process small portions of the contents of polyergic cells can grow out to new cells according to the number of energids they contain; in monergic cells such a breaking up is not possible.

[3] Monergic and polyergic are shortened forms for monenergidic and polyenergidic.

the time for propagation arrives. In land-plants the cellular structure is general and the several cell-chambers are separated from one another by firm walls. It is no part of our purpose however to describe here the inner structure of plants; what has been briefly stated is all that is necessary from the organographic point of view. It will be readily understood that there are many intermediate conditions existing between the categories just described; for example, amongst the Siphonocladiaceae the filiform branched thallus consists of polyergic cells.

We do not propose to depict here the relationships of configuration of monergic plant-bodies. It has been possible in a large number of cases to discover a relationship between their forms and their life-functions. We see this, for example, amongst diatoms. The monergic cells of fixed species have a different construction from that which obtains in the actively moving or floating species. It is also clear that the pear-like form of most swarm-spores is especially favourable for their movements. In other cases however we know so little regarding the special life-relationships of the plants that we are quite unable to speak with certainty; we cannot, for example, say whether the rod-like or sickle-like desmids have relationships of a kind different from those of the plate-forms.

Transitions from monergic to polyergic forms have been found in the most different cycles of affinity. They are brought about by the energids which arise in process of division remaining in union one with the other instead of separating. Naegeli[1] long ago described this as follows:—'The cells which in the simpler plants separate as germs and represent the beginnings of new individuals become in the next higher plants a portion of the individual organism and prolong the ontogeny in a corresponding degree.'

The degree in which the single energids are united with one another may be more or less intimate. A polyergic plant is either an *energid-colony* or *coenobium* (cellular or non-cellular) in which a division of labour between the several energids has not yet appeared and each energid is capable of living for itself; or the energids exhibit a division of labour and although in union with one another are therein different from one another—they form an *energid-dominion*. This is what has come to pass in the majority of the polyergic plants. There are of course many transitions between these two conditions, and their separation is in a measure artificial, being based upon extreme relationships.

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[1] Naegeli, Systematische Übersicht der Erscheinungen im Pflanzenreich, Freiburg i. B., 1853; Id., Mechanisch-physiol. Theorie der Abstammungslehre, p. 332.

I. COLONIES OR COENOBIA.

The outer form of the colonies is very variable. I shall here only cite a few examples in order to explain what we mean by them.

A. Colonies which are not fixed.

1. Colonies of naked energids, or, non-cellular energid-colonies.

We find these in the plasmodia of the Myxomycetes (Fig. 2). The advantage which the plant obtains by the possession of the colonial form is manifest when spore-formation takes place, and especially in spore-distribution. An energid-colony can construct larger fructifications which are better adapted for the distribution of the spores. It is especially instructive to note that in the Acrasieae, one of the lowest groups of this developmenta series, the vegetative energids remain single; they form no plasmodium and only with the approach of spore-formation do they creep together. In Guttulina, a member of the group, no fructification is even formed, and the only advantage we can suppose the plant derives from the creeping together of the energids, or of the heaping together of the spores, is that such spore-heaps offer a more favourable condition for the distribution of the spores than would be the case were the spores to remain isolated. If now, without further considering the utilitarian question, we assume that the originally free energids, which here may be termed amoebae, exercise an attraction, which is probably a chemotactic one, upon each other, we find that, starting from the Acrasieae, the Myxomycetes exhibit a progressive series in which the formation of spores is postponed to *a period gradually getting later* after the formation of the colonies, so that between

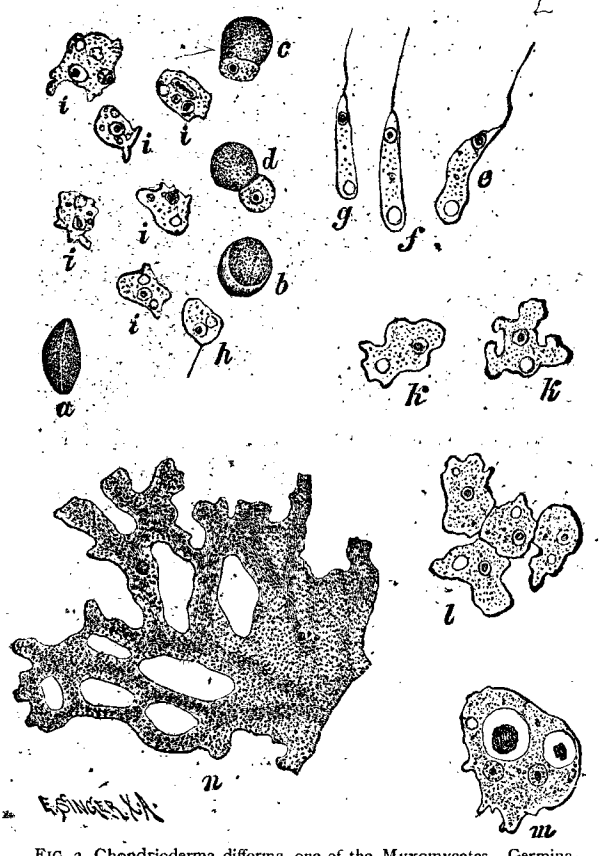

FIG. 2. Chondrioderma difforma, one of the Myxomycetes. Germination and formation of plasmodium. *a-h* spores and the naked flagellate energids which swarm out from them; *i*, *k*, the energids have become amoebae; *l* amoebae creeping together to form an energid-colony; *m*, *n*, older energid-colonies, the plasmodium; *a-m* magnified about 540; *n* magnified about 90. Lehrb.

the stage of formation of the colonies and that of the formation of spores a vegetative stage is intercalated; and this enables the number of spores formed to be greatly in excess of the energids which unite to form the colony, whereas originally, as in Guttulina, the number of spores and of energids is equal. In the most highly developed cases, even in the Acrasieae, a division of labour is found between the energids; a fructification is formed in which all the energids do not become spores, but only a portion of them, usually the larger, is devoted to this purpose, whilst the others are applied to the formation of a stalk.

Polysphondylium violaceum and Dictyostelium mucoroides, which have been minutely investigated by Brefeld[1], are very instructive forms. In these species naked amoeboid energids issue from the germinating spore and multiply by bipartition, but do not unite to form a plasmodium as in other Myxomycetes. It is only at the time of formation of the fructification that they aggregate together in uncommonly large numbers to form a dense mass, influenced no doubt by chemotaxy. A 'division of labour' now ensues. All do not become spores. The central portion of the mass of amoebae is devoted to the construction of a cellular stalk; the amoebae concerned in this absorb water from their neighbours, surround themselves with a membrane and become polyhedric cells. The stalk grows at its apex by the amoebae at this position becoming transformed into stalk-cells. The amoeboid mass creeps up the stalk to its apex, and when the formation of the stalk is completed all the amoebae which have not been employed in making the stalk become spores. Here all the amoebae are originally alike, and their position in the amoeboid heap and their reciprocal influence are the factors determining which of them shall become stalk-cells and which spores. The formation of the stalk is clearly of advantage for the distribution of the spores and it has the same function as in the sporogonium of a moss. One of these fructifications of Polysphondylium, growing at its apex by means of the new energids which creep up to it, furnishes a remarkable counterpart of a shoot of one of the higher plants which also possesses at its apex a vegetative point of embryonal tissue but below is composed of mature energids.

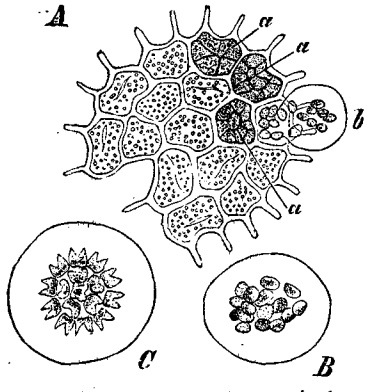

FIG. 3. Pediastrum granulatum. *A* colony all the cells of which are empty excepting four whose contents are forming daughter-colonies. *B* young colony with cells still irregularly placed. *C* somewhat older colony, the cells now arranged in one plane, the outer ones are evidently two-horned, the inner ones show only a trace of the horns. Magn. 300. After A. Braun. Lehrb.

2. COLONIES OF ENERGIDS INVESTED BY A MEMBRANE.

A few examples only which are instructive in connexion with general questions of organography will be cited here.

a. Protococcaceae. Figure 3 is a representation of a colony of Pediastrum

[1] Brefeld, Untersuchungen aus dem Gesammtgebiete der Mykologie, Heft 6.

granulatum, a common freshwater alga, in which most of the cells are shown emptied of contents. It will be noted that the cells around the margin of the table-like colony differ in form from the inner cells; each of them possesses two horn-like processes, or, to express it shortly, is two-armed. The inner cells have not these. But when the cells are aggregating to form the colony, as is shown in the young stage, Fig. 3, *C*, all the cells have the capacity to produce two arms; the inner ones are however prevented from assuming this form by the closeness with which they are packed together. Were the regular arrangement of the cell-colony hindered at its birth, all the cells would certainly be two-armed. Here then a *reciprocal influence*, not of a very far-reaching character, affects the cells. The single cells of the colony of Pediastrum are, according to Chodat, polyergic at an early period, and in the formation of a new colony the energids which proceed out of one cell separate from one another. What force brings about the expansion of the colony in *one* plane we do not know; perhaps the direction of rays of light has something to do with it.

b. A special interest attaches to the relationships of configuration of the colonies of Volvocineæ. Amongst them we find isolated monergic forms, like Chlamydomonas, with freely motile cells, and also more highly developed ones, like Volvox, consisting of colonies of many cells exhibiting a polarity and division of labour.

Chlamydomonas is a nearly ellipsoid or spherical energid possessing a membrane and provided with two cilia, and it multiplies by division. In Chlamydomonas Brownii, for example, four daughter-cells, seldomer two, are produced in asexual propagation, according to Goroshankin. A cell which is about to divide becomes motionless, and then a longitudinal wall is formed within it, followed by a second at right angles to the first. The four daughter-cells then separate from one another. They lie in one plane and would make a four-celled colony such as occurs in Gonium[1] were they to remain united. The colony in this genus is flat and table-like, built up out of four to sixteen quite similar cells which are surrounded by a common gelatinous envelope, but are not, as was formerly supposed, in connexion with one another by protoplasmic continuations. How slightly the cells are united with one another is shown by the fact that in Gonium pectorale, as Bütschli states, single cells often leave the colony and swarm around it, each having all the appearance of a Chlamydomonas; frequently also the colony breaks up entirely into isolated cells. Each of these cells may become the foundation of a new colony, but once the colony is formed a vegetative increase of the cells no longer takes place. If we imagine one of the flat colonies of Gonium invaginated to a hollow sphere we should obtain the colonies of Eudorina, and the colonies of Pandorina arise in a manner only slightly different; in these genera also all the cells of the colony are equal in value, and are not in continuation one with the other. Volvox[2] itself differs from these. In the first place the

[1] See Migula, Beiträge zur Kenntniss des Gonium pectorale, in Botan. Centralblatt, xliv (1890).

[2] See specially Klein, Morphol. und biolog. Studien über die Gattung Volvox, in Pringsh. Jahrb. xx; Id., Vergl. Unters. über Morphologie und Biologie der Fortpflanzung bei der Gattung Volvox, in Ber. der Naturf.-Gesellsch. zu Freiburg i. B., Bd. v (1891), where the literature is cited.

number of its cells is much greater, and so is the size of the whole colony. In Volvox aureus (Fig. 4) the number of cells varies between 200 and 3,000, in V. globator the number in the asexual colonies, which are the only ones now under consideration, varies between 1,500 and 16,400. The remarkable inner structure of the colonies in this genus cannot here be described, suffice it to mention that they possess two poles which are distinguished as well by the history of their development as by their ultimate structure. The one of these, the *trophic* pole, which is in front when the colony is in motion, marks the point at which the union of the cells took place by which the sphere was produced out of a concave surface, and sometimes an opening may be found at this point. The cells in the vicinity of the trophic pole are nourishing cells, whilst the posterior half of the colony consists of cells by which the function of propagation is performed, this being limited in each colony to either the sexual or the asexual method. The cells at the anterior pole have a very large red eye-spot, the stigma, which evidently plays a part in the disposition of the movements of the colony, and these eye-spots diminish in size in the cells towards its equator, and disappear altogether in those on the posterior half or are replaced by a colourless oil-drop. In the posterior half of the colony all the cells are not propagative cells—in Volvox globator there are usually only eight of these; the function of the other cells is purely nutritive, and at a later period they perish, being probably used up by the propagative cells, and in correspondence with this their protoplasmic body stops growing during the development of the propagative cells, and becomes poor in substance. This far-reaching influencing of one cell by another is explained by the fact that there are protoplasmic continuations between the cells, and these are more numerous between the cells in the posterior generative hemisphere than in the anterior trophic one. In Volvox then a division of labour has taken place; first

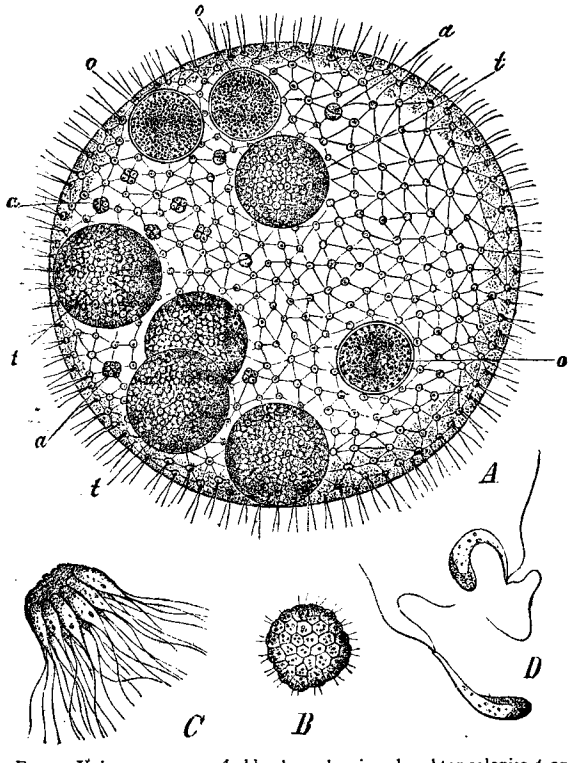

FIG. 4. Volvox aureus. *A* old colony showing daughter-colonies *t*, and antheridia *a*, and eggs *o*. The cells appear as small circles upon the surface of the sphere. Magn. 180. *B* young colony. Magn. 687. *C* young colony seen from the side. *D* isolated spermatozoids. Magn. 824. After Klein. Lehrb.

within the vegetative cells, inasmuch as the anterior ones are somewhat differently organized from the posterior; and secondly between generative and vegetative cells. The vegetative cells work for the generative cells and then disintegrate, and thereby the colony is able to multiply itself rapidly under favourable conditions, and to send strong daughter-colonies into the world. As a matter of fact there is under such conditions an uncommonly productive multiplication. In the colonies of other Volvocineae the cells exercise a reciprocal influence though it is less profound, and it is shown in their common swimming movement which of course presupposes a regulating of the ciliary capacity of the single cells. It is because the relationship of Volvox to the colonies of other Volvocineae is so clear that we reckon it as a colony; considered by itself one might regard Volvox as a true pluricellular plant and term it a cell-dominion. There is no experimental evidence as yet available which would enable us to say whether in the event of the destruction of its generative cells any other cell could take up their work; but it is probable if the destruction took place without any great injury to the colony, and at a sufficiently early period, that this substitution would occur. I do not here intend to describe the organs of propagation in the Volvocineae, I will only recall the fact that we find in the group a very instructive series of gradations from isogamy to oogamy. The spermatozoids of Volvox present a parallel formation with the spermatozoids of Archegoniatae; their elongated form is, in my view, developed here, as there, to enable them to pierce into the gelatinous coating of the ovum.

B. Fixed Colonies.

These are attached to the substratum either through the excretion of fixing substance, or through the construction of special anchoring organs which frequently appear in consequence of external stimuli, the so-called contact-stimuli, and perhaps owe their origin primarily to such a sensitiveness. The existence of an anchored base is a further stage of differentiation of the colony, which may then readily pass into the condition of a cell-dominion if the end of the colony opposite to the base acquire the form of a vegetative point. This step has indeed frequently been taken, but I must first of all depict some examples in which it has not taken place.

The colonies of Apiocystis, which are invested by a common gelatinous envelope, excrete at their base a fixing substance in the form of a kind of disk. The peculiar 'pseudo-cilia' of this alga which stretch out from the gelatinous envelope I consider to be organs for the interchange of material, especially of gases, because the thick gelatinous envelope makes this process difficult.

Amongst the Diatomaceae occur colonies, both free-floating and fixed, of the most different forms, in which the single cells are held together usually by a gelatinous excretion, and this excretion serves as the anchoring substance in the fixed colonies. A division of labour among the cells of the colony is not known unless we see this in the circumstance that in many of them, as for example in the genus Achnanthes, the thread-like colonies are fixed at one end of the thread and their basal cell alone excretes the mucilage for fixing the organism. This

cell behaves therefore differently from the other cells of the colony, but at the same time each one of these is able to take over the work of producing adhesive mucilage.

In Licmophora flabellata, Ag. (L. radians, Kütz.), which is represented in Fig. 5, a different construction of the single members of the colonies is only apparent. The cells here sit in a fan-like arrangement upon the somewhat broadened end of a branched gelatinous stalk, the branches of which differ in strength. Some are short and thin and carry only few cells, others again are much thicker and longer and bear many cells. This appearance is explained by the fact that the gelatinous substance is excreted at the under end of the cells and that single cells may separate themselves from the others; as they separate they build with their gelatinous excretion a new stalk which must be necessarily thinner and shorter than that which belongs to a larger number of cells. A structure is produced in this way which may be very like a monopodial system of branching, but the similarity is only superficial, for the cells are all equal and the separation of single ones is not a regular process. The case would be very different if the cells of the 'side-branches' were after some time to lose their capacity for growth and division, whilst those at the top of the chief axes retained these powers. There is however neither an external nor an internal ground for assuming this in these cells which are bound together only by a gelatinous *envelope* [1].

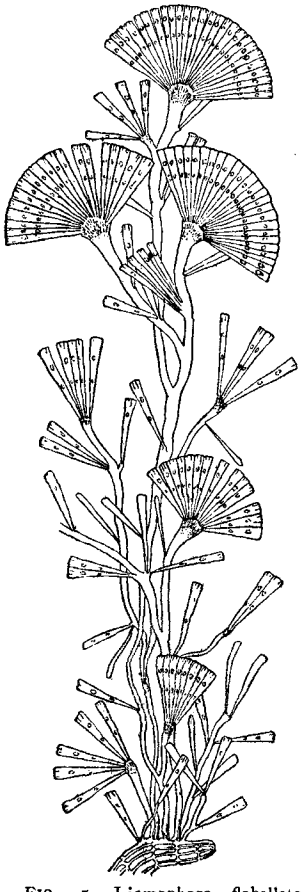

FIG. 5. Licmophora flabellata. Diatom-colony with branched gelatinous stalk. After Smith.

The algal genus Hydrurus supplies an illustration of special prominence. The plants in this genus consist of richly-branched gelatinous threads, sometimes many metres long, which are frequently found in freshwater streams and rivers. There is really here a greatly developed colony of brown Flagellatae, and one can easily recognize that every cell has five or six pulsating vacuoles like those which occur otherwise only in swarm-cells. The single energids are embedded in a gelatinous substance, and even in the germination of the propagative cells the secretion of the slime is considerable upon that portion of them which is turned towards the substratum where it forms a fixing organ (Fig. 6, *I*). The energids

[1] Similar branching is observed in Nevskia ramosa, a remarkable Schizomycete; see Famintzin in Bull. de l'Acad. de Sc. de St.-Pétersbourg, nouv. sér. ii (xxxiv), 1892, p. 481. For an account of the interesting formation of colonies in Myxobacteria see Thaxter, in Botanical Gazette, 1892; a division of labour appears in the plants so that all the cells of the colony are not equal in capacity of development.

of the colony all behave at first in like manner; all can grow out into branches, and thus perfectly irregular branching may take place (Fig. 6, *III*). But there is a difference between the branches and the chief stem—it is only the energids of the branches which can become propagative cells[1]. The chief stem apparently serves only as a mechanical support for the whole, and it dies off at a later period. The capacity for development of the energids at its base has evidently become modified, because the claims made upon the chief stem as a mechanical support are quite different from those laid upon the lateral branches—living in quickly flowing water the energids have changed their nature through the changed demands made upon them. The growth of the branches is also remarkable. At the apex the gelatinous layer is thinner and an energid is found here which, according to Klebs, divides by a longitudinal wall; after this it is displaced and another energid occupies the apex. Whilst then the single energids are like one another in all essentials, the apex of the colony always has a different structure from the part lying behind it. This is at least an approach to the formation of a vegetative point. Probably also the threads of many filamentous Algae such, for example, as the Oedogoniaceae, Confervaceae, and others, are nothing else than colonies of swarm-spores which for a time are invested with a membrane. The basal cells of these threads, which grow out to fixing organs, behave usually like the basal portion of the chief stem of Hydrurus, that is to say, they are deprived of their capacity for development. In Ulothrix zonata, for example, the protoplasm in the basal cell frequently dies and thus divisions altogether cease in it whilst the other cells all go on dividing as before (Fig. 7). The reason for this phenomenon may be the same as that which we have above attempted to establish for Hydrurus.

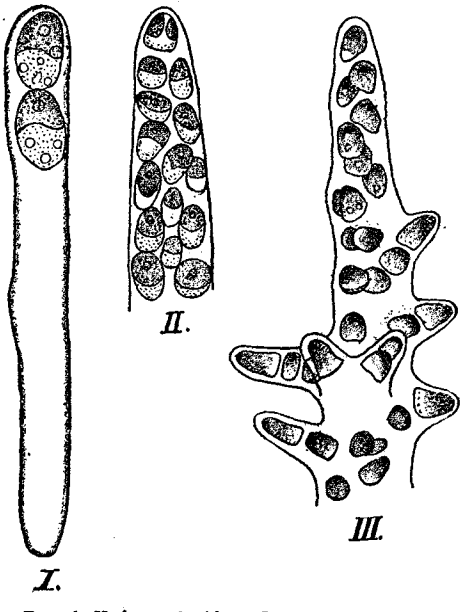

FIG. 6. Hydrurus foetidus. *I* young plant. *II* apex of a plant; chromatophore of the end-cell already divided. *III* branching. *I* and *II* after Klebs, *III* after Berthold.

The examples with which we have just dealt show us that, starting from colonies of similar cells or energids all of which are capable of further development, an attempt is made in different directions to secure a higher differentiation as this is expressed in the division of labour

[1] See G. Klebs, Flagellatenstudien, in Zeitschr. f. wissensch. Zool. lv (1892), pp. 265, 353. The literature is given here.

between the inhabitants of the colony. The term 'division of labour' of course explains nothing, it is merely a comprehensive expression for the facts. The division of labour and the differences bound up with it are brought about firstly by the reciprocal influence of the energids of a colony and then by their different relations to external factors. Energids are frequently, on account of their *position* in a colony, influenced by other energids, for example, in Pediastrum, Polysphondylium, and Volvox, and are thereby fixed in their form and function; they are further, on account of their position, differently affected by external

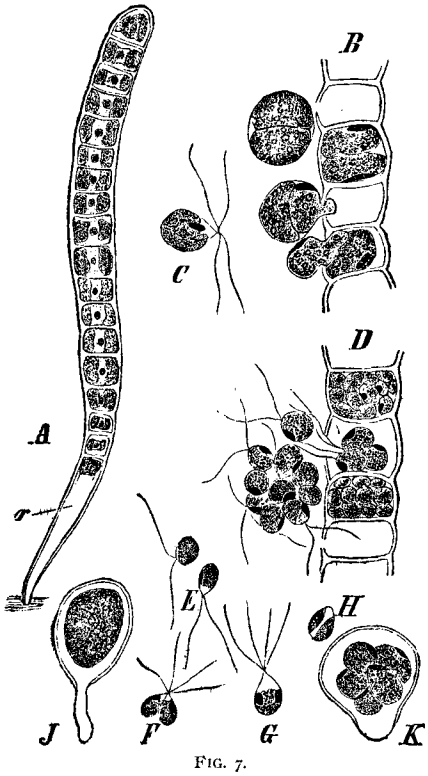

FIG. 7.

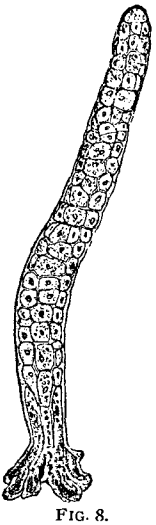

FIG. 8.

FIG. 7. Ulothrix zonata. *A* germ-plant, *r* anchoring organ which is poor in chlorophyll or has entirely lost its chlorophyll. Magn. 300. The other figures do not concern us here. After Dodel-Port. Lehrb.

FIG. 8. Ulva lactuca. Germ-plant with anchoring organs at base. Magn. 220. Lehrb.

factors, and react differently to external stimuli, as we have seen in Hydrurus.

An extensive division of labour can only be expected in branched vegetative bodies. Branching occurs, as we have seen, even in colonies, but it is regular only where a *vegetative point* exists, and the possession of this is characteristic of cell-dominions and therefore of all 'typical' plants.

II. CELL-DOMINIONS WITH VEGETATIVE POINTS.

We owe the special term *vegetative point* to the founder of the history of development, Kaspar Friedrich Wolff[1], who endeavoured to establish by direct observation the origin of organs—their *generatio*—instead of accepting the speculations of the theory of evolution prevalent at his time. Through this method he came to the conclusion that in development an actual *new formation* of parts occurs, a new laying down of organs on the originally undifferentiated germ. To this result he was led by his investigation of the development of the leaf, as well as of the flower, in the bean. He recognized that the existence of primordia of leaves in the bud, upon which the doctrine of evolution was based, afforded only a narrowly limited foundation. If you examine accurately a bud 'donec tandem hoc modo introrsum et deorsum simul penetrando ad substantiam plantae interiorem pervenias, humidam, succis gravidam et nulla amplius folia tenentem' and you will arrive at 'extremitas axeos trunci' where no differentiation of tissue yet exists. He calls this termination of the stem-axis or twig-axis the vegetative point, and upon it arise the primordia of leaves and lateral branches as 'propulsiones trunci.' In this way one of the fundamental facts in the development of plants was clearly established, namely, the plant-body possesses places where, to use the expression of Sachs, 'embryonal' tissue still exists which furnishes new cells and new organs. This is a feature which distinguishes them at once from the higher animals. New organs usually arise in such a way that the youngest are nearest the vegetative point; they are in progressive serial succession. A study of what may be observed in the lower plants shows that there is little constancy in this respect, and also that the possession of a vegetative point different from the other parts is only a special case, although at the same time the most widely spread one, of the possible constructions of the plant-body. We have already seen in Hydrurus an approach to a vegetative point; a real vegetative point however requires that the cells composing it should behave differently from those which are found behind it, and that the primordia of the lateral formations should develop from the vegetative point in a definite and regular succession.

Amongst the species of Cladophora, one of the most widely spread genera of the branched pluricellular filamentous Algae, we find a considerable advance in this respect. The individual cells are here polyergic, but this is of no consequence for our present purpose. In Cladophora fracta[2] cell-multiplication takes place by the division of a cell occupying

[1] K. F. Wolff, Theoria generationis, 1758.

[2] See Berthold, Untersuchungen über die Verzweigung von Süsswasseralgen, in Nova Acta Acad. Leop.-Carol. xl (1878).

its apex, the apical cell, and the branches, which are constructed like the chief axis, arise in progressive serial succession from the cells thus produced. At a later period division begins also in these segment-cells, and from the new cells thus developed branches are formed which are intercalated between those previously existing. If we suppose now that this formation of intercalary branches is suppressed, as is the case in other species of Cladophora, for example in C. prolifera (compare Fig. 9), we should retain the scheme of formation of lateral organs which is the most widely spread amongst plants, namely, that of the progressive origin of new formations.

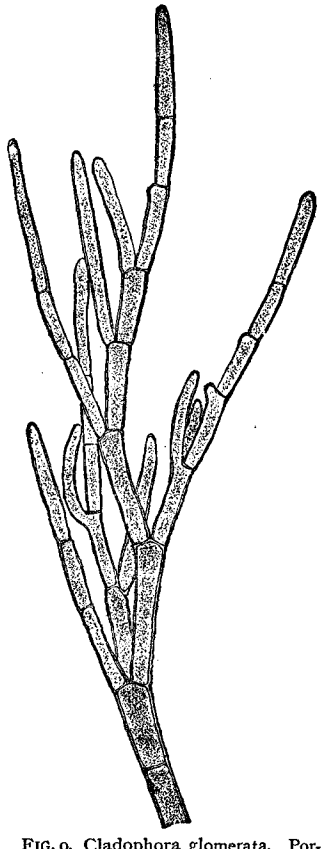

FIG. 9. Cladophora glomerata. Portion of thallus. The branching is in regular progressive serial succession towards the apex. Magn. 48. Lehrb.

A difference between the construction of chief axis and of lateral shoots is often concurrent with the branching, as has been already pointed out in the case of Hydrurus. The chief axis has, as in that species, to discharge a mechanical function different from that belonging to the lateral axes and it also stands in a definite metabolic relationship to them—it supplies material to the lateral axes and at the same time draws upon them. When the lateral axes are pressed closely together and envelope a chief axis they make the work of assimilation more difficult for it because they intercept the light. It is not surprising therefore that we meet with differences between chief and lateral axes. We find this, for example, amongst Algae which are copiously branched, like Draparnaldia and Chaetophora; at a certain age of the plant when the cells of the lateral axes continue an undisturbed growth, those of the chief axis are incapable of dividing, of producing swarm-spores, and of assimilating in a comprehensive manner, and similar phenomena may naturally be repeated between lateral axes. As the plant-body increases in size there is, as Herbert Spencer[1] has so well said, a tendency to the development of an inequality between its members, and this shows itself especially in a difference between chief axes and lateral axes.

Besides this we not infrequently observe in the Algae that the cell which gives rise to a branch lags behind the others in its growth either

[1] Herbert Spencer, Principles of Biology, i. p. 214.

temporarily or permanently. If this happens regularly the chief axis itself will exhibit a differentiation; the places upon it whence lateral organs spring, the *nodes*, behave differently from the internodes, and the difference is in many cases extremely sharp, for example, in Chara (Fig. 10). The cause of this may perhaps be that the formation of a lateral organ originally brought about a direct arrest of the zone of the chief axis from which it sprang.

We have thus arrived at a plant with a vegetative point and a regular evolution of lateral organs; we have further seen how, frequently through the branching, a more or less marked difference between chief axis and lateral axes may be brought about; and we have now to examine the different constructions of the lateral axes themselves.

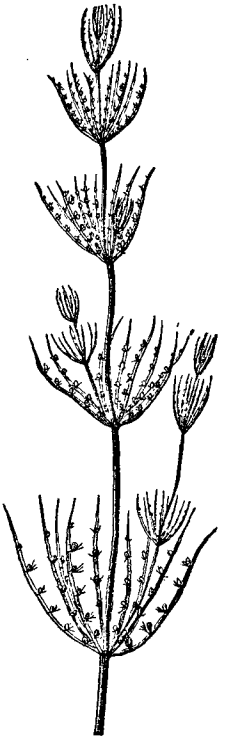

FIG. 10. Chara fragilis. Portion of shoot. The whorled 'leaves' which bear the sexual organs are short shoots. Natural size. Lehrb.

It is not at all unusual to find lateral axes distinguishable into long shoots and short shoots. The *external* differences between the two kinds of shoots are a consequence of the fact that the long shoots have unlimited growth whilst the short shoots have limited growth and therefore appear like arrested conditions of the long shoots. A difference of function however is bound up with this external difference in form; the long shoots are the instruments of the special branching of the plant; the short shoots are chiefly organs of assimilation. Thus in Chara the 'leaves' which are arranged in an apparent whorl are merely short shoots which differ also from the long shoots in having a simpler structure. We shall meet with these differences again among the higher plants; it will suffice to recall here as examples the well-known relationships of configuration of species of Pinus and of many Cacteae.

Alike in the higher and lower plants the short shoots and the long shoots primarily differ only quantitatively not qualitatively. A lateral axis which may develop into a long shoot under favourable conditions will, under unfavourable conditions, become a short shoot. In those cases in which long shoots and short shoots are more sharply separated their place of origin is also different, and there is besides an increase in the difference in structure which they exhibit. A few illustrations of this may be given.

The Sphacelarieae[1], which belong to the Phaeophyceae, furnish us

[1] See Geyler, Zur Kenntniss der Sphacelarieen, in Pringsh. Jahrb. iv. p. 479; Pringsheim, Über den Gang der morphologischen Differenzierung in der Sphacelarieenreihe, Gesammelte Abhand-

with an instructive illustration of the different gradations of form amongst individual organs. As we can here only refer to a few examples we must limit ourselves to the formation of the branches.

In the genus Sphacelaria itself the plant consists of axes which are built up out of many rows of cells. They branch, producing many lateral branches which in some species are all alike, in others appear as short shoots and long shoots. They possess also 'hairs,' that is to say, outgrowths of limited growth which remain as simple rows of cells poor in protoplasm and are laid down in a different manner from the ordinary branches, inasmuch as they arise so near the apex of the axis that at their origin the apical cell is pushed to one side. In Halopteris filicina the 'hairs' are wanting (Figs. 11 and 12), and the richly-branched

FIG 11. Halopteris filicina. Shoot-system. The darker parts at the ends of the shoots are the apica cells. From a micro-photograph. Slightly enlarged.

thallus is composed entirely of long shoots and short shoots of different orders. They are all, as is shown in Fig. 12, laid down in like manner quite close to the apex. Each shoot ends in an apical cell, and is usually distichously branched so that a feather-system of branching is produced. The branches of different order are distinguished by the fact that the higher a shoot is in the order of branching the smaller is its apical cell and the earlier does it end its growth and pass into the

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lungen, Bd. i.; Magnus, Zur Morphologie der Sphacelarieen, in Festschr. zur Feier des hundertjährigen Bestehens der Ges. naturforsch. Freunde zu Berlin, 1897; Reinke, Beiträge zur vergl. Anatomie und Morphologie der Sphacelariaceen, in Biblioth. botanica, Heft 23.

permanent condition[1]. Thus in Fig. 12, whilst in the axis of first order the whole of the cells are repeatedly divided by longitudinal walls, this process is suppressed in the axes of higher order step by step, and many of them remain as simple cell-rows and appear in relation to the others as formations *arrested* at different stages of development. We further learn from Fig. 12 that the first branch upon all the lateral shoots is formed on the side next the mother-shoot, and that the first two lateral branches are always upon the same side—an arrangement which makes it possible for all the lateral shoots to occupy their respective positions without covering one another; occasionally it is true such covering occurs, but if the branches from the beginning were regularly distichous covering would be a *necessary* result. The lowermost branches are often arrested in their development; the differences between long shoots and short shoots are therefore here only quantitative not qualitative.

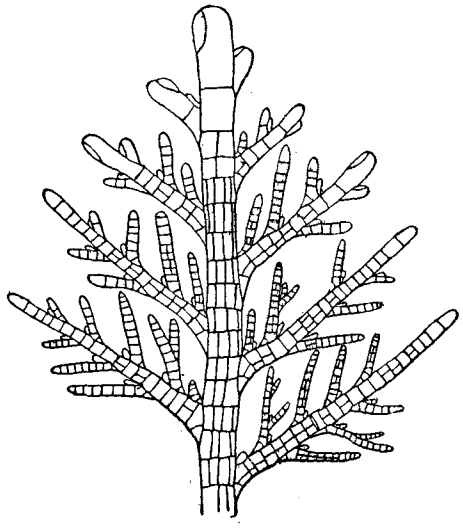

FIG. 12. Halopteris filicina. End of a long shoot. Segments are cut off from the large apical cell by curved walls and they grow into branches of the first order. These branches repeat the process. The lateral branches of higher order develop successively less strongly.

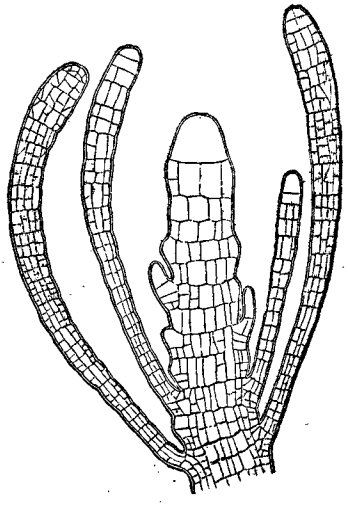

FIG. 13. Cladostephus verticillatus. Longitudinal section through a long shoot with short shoots. The short shoots have limited growth; the apical cell of each becomes by division transformed into a cell-mass. After Pringsheim.

Cladostephus, which however cannot be phylogenetically derived from Halopteris, shows a higher differentiation and possesses also a higher anatomical construction. In it we find the following members:—

1. Long shoots. New long shoots arise through a peculiar forking of the apex.

[1] Similar differences occur in the shoot-system of higher plants. In the silver fir, for example, the vegetative points of the different shoot-forms are different. The bud of the chief stem is short and compressed, has a bulky primordium, &c., and is therein distinct from the buds of both the long shoots and the short shoots; buds of short shoots may however be caused to develop as long shoots, and long shoots may become chief shoots. See, with reference to the form of the different vegetative points, Busse, Beiträge zur Kenntniss der Morphologie und Jahresperiode der Weisstanne, in Flora, lxxvii (1893), p. 113.

2. Short shoots. These are placed in a whorl and arise from the oldest cortical cells of the stem. Pringsheim called them 'leaves,' and from the outset they are laid down differently from the long shoots. See Fig. 13.

3. 'Fructification leaves.' These are short shoots which bear the propagative organs. They are generally like the 'leaves' but are distinguished from them by a simpler anatomical construction and by their position, for they are formed specially at the end of the period of vegetation in a regular way on the older segments of the stem.

4. 'Hairs.' These are rows of cells which are formed on the 'leaves.'

5. Adventitious shoots. These proceed from the central cells of the axis[1].

The point that first strikes one here is that the different members are different in their origin, and this is not the case in Halopteris.

An analogous differentiation of long shoots and short shoots is found also in many Florideae, and some examples of this which will illustrate well the division of labour among short shoots may be here briefly cited. I select for the purpose some freshwater-forms which are found at the mouths of rivers in Guiana attached to the mangroves and other swamp-plants[2].

Bostrychia Moritziana is a floridean alga with a feathered branch-system. The axes which are constructed to support the branch-system are cell-masses of a more complex structure than the ends of the branches, which are merely cell-rows. The chief axis however ends in a cell-row. The feathered branches have a limited growth and they appear as short twigs of different orders which are arrested at an earlier or later stage of development. The branching at the apex appears to be forked, but it is really monopodial. The lateral twig arises in the apical cell by the separation through a long dividing wall of a segment which grows out to form it, and is at first as strongly developed as, and pushes to one side, the continuation of the chief shoot and appears itself to be this continuation. The same process is repeated in the branching of each member except in the case of those which are destined to form organs of attachment or of propagation. The plants are firmly anchored to the substratum by special unbranched members of the thallus which produce at their apex the actual fixing organs, usually termed rhizoids. These members of the thallus, which are the branches marked *W* in Fig. 14, have a structure and a direction of growth different from what is found in the vegetative twigs. They are, in the mature condition, cell-masses right to the apex, although they are laid down as cell-rows, and they bend towards the substratum. They appear at an early period inserted upon the under side of the branches, and in consequence of this the whole vegetative body has the character of a dorsiventral shoot-system with roots on its under side. The basal branch of one of the short assimilation-shoots shows this best. We must further note that the planes of branching of the assimilation-shoots do not always coincide. In addition to this method of formation of shoots another occurs: isolated unbranched shoots become club-like cell-masses or stichidia, as they are called, which produce the tetraspores.

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[1] I say nothing here of the root-threads.

[2] Goebel, Über einige Süsswasserflorideen aus Britisch-Guyana, in Flora, lxxxiii (1897), p. 436.

It is of interest that three other plants growing in the same locality as the one just mentioned present a quite similar differentiation of their organs. Bostrychia callipteris has fixing shoots like those of Bostrychia Moritziana; in Lomentaria impudica the shoots for attachment stand upon the under side of the branch-system between two lateral shoots and are not unfrequently provided with outgrowths; Delesseria Leprieurii forms no twigs as shoots of attachment, but produces tufts of rhizoids just below each apparent fork of the thallus which perform the same

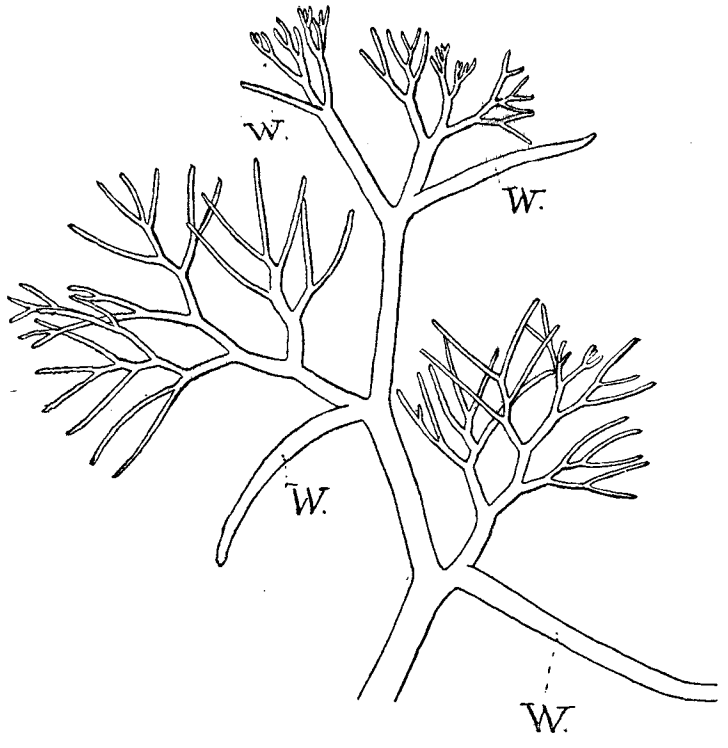

FIG. 14. Bostrychia Mortiziana. Habit of a shoot. The shoot-axis bears branched short shoots which serve as organs of assimilation, and unbranched shoots, *W*, turned to the substratum by which the plant is fixed. Magnified.

work, and they are absent from the shoots which bear tetraspores. In all these cases the organs of attachment arise without the influence of an external stimulus, shoots for this definite purpose are laid down as such; but in Plocamium (Fig. 15) the development of a shoot into a fixing organ depends entirely on whether its apex comes into contact with a fixed body or not.

Here then also through simple stages of formation of organs a differentiation comes about which represents the root[1] and leafy shoots of the higher plants. This similarity is all the more striking when the short shoots take on an external leaf-like appearance. Polyzonia jungermannioides, for example, shows, as its specific

[1] In Bostrychia Moritziana the down-growing twigs are the analogues of roots.

name indicates, the features of a foliose liverwort even to the oblique position of its 'leaves' (Fig. 17). That these 'leaves' are expanded short shoots is shown by a comparison with Cliftonaea pectinata (Fig. 16), another member of the Florideae, in which (see the left side of the figure) two rows of short shoots are visible.

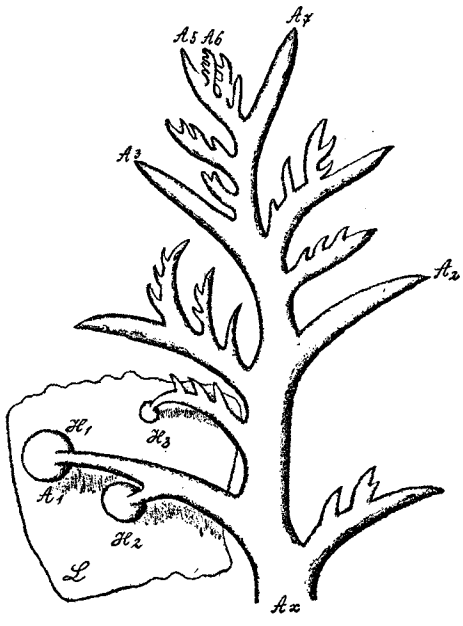

FIG. 15. Plocamium coccineum. The apices of the branches at H_1, H_2, H_3, have developed adhesive disks by which the plant is attached to another alga, L.

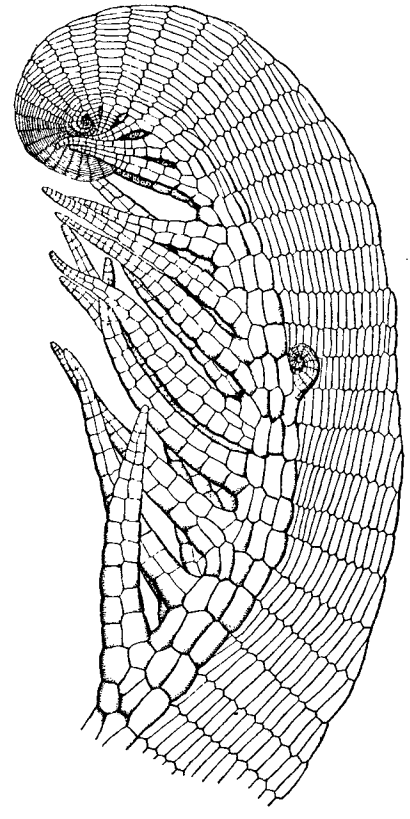

FIG. 16. Cliftonaea pectinata. End of a shoot. The short shoots corresponding to the leaves of Polyzonia stand approximated to the under side (left). Magnified.

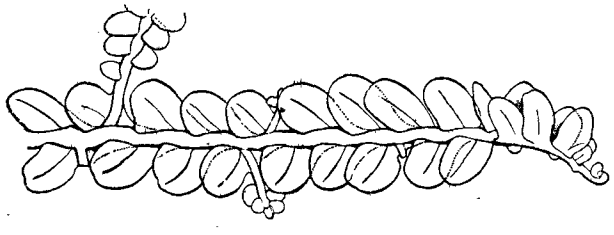

FIG. 17. Polyzonia jungermannioides, one of the Florideae. Habit of plant. Viewed from above, except on the right where a portion is seen in side view. Slightly magnified.

In Polyzonia also there is an axillary position of the lateral shoots which is the rule in the higher plants; each lateral shoot arises at the base of a 'leaf.' A similar relation between short shoots and long shoots occurs also in other Florideae [1].

[1] See Kny, Über Axillarknospen bei Florideen. Berlin, 1873.

IV.

NORMAL FORMATION OF ORGANS AT THE VEGETATIVE POINT AND REGENERATION.

The manner in which organs are laid down at the vegetative point requires no comprehensive exposition here [1]. I may however note the following chief facts :—

1. On vegetative points, whether these be terminal or intercalary, which have an unlimited capacity of growth, the primordia usually arise in progressive serial succession ; they are lateral outgrowths, exogenetic or endogenetic. In many cases, for example monocotyledonous embryos and the Lemnaceae, a clearly limited vegetative point generally does not exist [2].

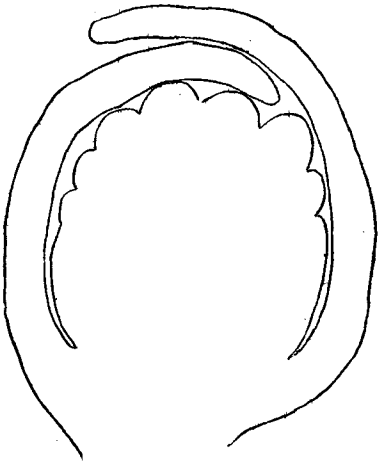

FIG. 18. Vallisneria (Lagarosiphon) alternifolia. Longitudinal section of a young inflorescence. The flowers are laid down in descending serial succession.

2. In the flower-region the vegetative point is sometimes completely used up in the formation of the leaf-organs arising latest from it. Members in this case are *terminal.* A like condition is found in the development of the antheridia and archegonia of many mosses.

3. On shoot-axes which have limited growth, and in primordia of leaves, the direction of the serial succession of the primordia of organs depends upon what part of the vegetative point retains longest its embryonic character. If this part should be at the base then the serial succession of the development is basipetal (see Fig. 18), or, as is the case with the primordia of the lateral leaflets in many leaves, as well as with the ovules upon some placentas, the development proceeds from the middle to the apex and base. Intercalation of new primordia of organs between those already existing takes place amongst the higher plants only in the region of the flower.

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[1] Compare the chapter upon this subject in my 'Vergleichende Entwicklungsgeschichte der Pflanzenorgane,' p. 177.

[2] See Part II of this book.

4. The vegetative points act as attractive centres for plastic material, their influence being stronger or weaker according to their position. If, for example, the vegetative point of the prothallus in a fern be destroyed or cut away, numerous 'adventitious shoots' spring from the prothallus which could not have arisen so long as the vegetative point was active (see Fig. 20). In a plant with many vegetative points there is therefore frequently a kind of competition between the vegetative points—a phenomenon of which we shall speak when we deal with 'correlation[1].'

The formation of organs at the vegetative point is the normal relation. Mature cells which have once entered as elements into the construction of a definite portion of a plant-body are incapable of further development if vegetation is not disturbed. They have however frequently not yet lost the capacity of other development, but this usually exists only in a latent condition and is only called forth when the reciprocal influence of the cells is annulled. This is what happens in the phenomena which are commonly grouped as regeneration. I purposely avoid the expression 'adventitious formation' because very different things are understood by that. When, for example, the buds which appear upon the leaves of many ferns, such as Asplenium bulbiferum and others, and amongst the Spermaphyta in Bryophyllum calycinum, as well as those which are formed upon an old severed leaf of a Begonia, are all of them termed 'adventitious,' such terminology is pointless. The shoots in the first examples arise upon quite the youngest stages of the leaves so long indeed as their tissue retains an embryonal character; they appear at definite places, and belong throughout to the normal course of development of the plant. If we call these leaf-born shoots adventitious, all that we say is that they are absent from the leaves of most other plants. In the last-mentioned instance, on the other hand, the buds are produced from cells which have already passed into a permanent condition and whose definite peculiarities have been already acquired, and it is only structures such as these that we can call in the strict sense of the word 'subsequent' or 'adventitious.' The formation of buds in the ferns to which we have referred above is a part of the normal sequence of their formation of organs, just as shoots are regularly produced in progressive serial succession on the roots of Podostemaceae.

When speaking here of the new formation of organs which takes place on severed parts of plants or upon injured plants as regeneration, I leave out of consideration phenomena of callus-formation, healing of wounds, &c., which belong to the province of anatomy. The relationships of correlation which so often play an important part in regeneration will be dealt with in our Fifth Section.

[1] See the Fifth Section.

I. REGENERATION OF THE VEGETATIVE POINT.

Regeneration obviously takes place most easily in embryonal tissue, and it is of interest to note that those parts of the vegetative point are able to share in it which by their position in the higher plants we know to be already on the way to produce definite systems of tissues. After Ciesielski had first observed that a new root-apex appeared after some days upon roots whose tips had been cut off, Prantl[1] made a careful investigation of the process. He found that a complete restoration of the root-apex, in which all the layers of tissue have a share, takes place if the cut is carried through that point where the curved arrangement of the cell-rows of the vegetative point of the root passes over into a straight one. A slight growth takes place by which a 'callus' of embryonal tissue is formed, and in this a new vegetative point for the root subsequently appears in the position of the old one, so that the new root-apex has quite a normal appearance. Occasionally instead of one apex two may be developed, and it would be of interest to know, could it be determined, under what conditions this is brought about. If the cut is carried through at a further distance from the root-apex there is no restoration of the lost point, but primordia of one or more rootlets proceed from a growth of tissue which develops from the primordia of the procambial bundles. If the cut be still further from the point there is generally no regeneration at all, and this I believe is connected with the fact that in such positions the primordia of the lateral roots are already existent and one of them takes on the function of continuing the chief root, and therefore restoration of the chief root is suppressed. When the new vegetative point continues the root in the place of the old one, it must obviously do this under the influence of such parts of the old root as remain behind. If a root be split longitudinally the halves regenerate themselves, provided that they retain a portion of the apical region[2].

The prothalli of ferns behave in quite the same manner. If we split longitudinally the heart-shaped prothallus of one of the Polypodiaceae and remove a lobe, a regeneration of the vegetative point takes place; a new lobe is then formed out of the restored vegetative point and the prothallus acquires the original form again in its anterior portion, whilst no restoration of the older parts that were removed takes place. This incapacity to repair mutilations in old parts, which distinguishes plants

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[1] Prantl, Untersuchungen über die Regeneration des Vegetationspunktes an Angiospermenwurzeln, in Arbeiten d. botan. Instituts in Würzburg, Bd. i.

[2] For anatomical relationships, see Lopriore, Über die Regeneration gespaltener Wurzeln, in Nova Acta Acad. Leop.-Carol. lxvi. No. 5.

from many animals, especially the lower forms of these, is obviously a consequence of the existence in plants of the vegetative point; for new organs can arise independently upon the vegetative points and the restoration of a severed portion of a leaf, for example, would be of no use to the plant; but in animals, which possess no vegetative point, the loss of an organ would be a permanent injury were there no power of regeneration of the lost part.

II. NEW FORMATION OF ORGANS IN REGENERATION.

The cases we have just cited lead up directly to another series in which we do not find restoration of the lost parts but replacement of them by newly formed ones; the injury here seems to act as a stimulus. An example has been already given above in the case of roots in which the cut is made too far from the root-apex so that regeneration of the vegetative point cannot take place, and then on the cut surface substitution-roots appear. We find this also in seedlings of peas[1] when the root and hypocotyl are cut off below the point of insertion of the cotyledon; a callus is then formed out of which one or sometimes more roots arise, and in the latter case there is often a malformation through the 'concrescence' of two or more roots. When the shoot of a seedling plant of this kind is cut off there appears on the surface of the wound in many cases a callus only, in others however one or two shoots spring from it, and the opportunity to observe a similar development is often afforded on stools of Beech, Poplar, and other trees, where a callus arises from the cambium and from it a large number of shoots sprout.

During their progress to completion as entire plants portions which have been severed from plants very often exhibit the phenomena of 'polarity[2],' which of course existed previously in the uninjured plants and only becomes more apparent in the regeneration. I can only make a brief reference here to these phenomena.

On a piece of shoot which has been cut off from the parent plant the primordia of roots develop first of all at the root-pole, that is to say, on that portion which is furthest away from the vegetative point of the piece of shoot; from the shoot-pole shoots proceed. Roots, so far as they are generally capable of regeneration, behave in a contrary manner[3]. Leaves show no polarity; in them the new formations arise at the leaf-

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[1] Vöchting, Über Organbildung im Pflanzenreich, ii. p. 19.

[2] See Vöchting, Über Organbildung im Pflanzenreich, i and ii; Sachs, Stoff und Form der Pflanzenorgane. Gesammelte Abhandlungen, ii.

[3] There are certainly some exceptions to this. One, relating to the tubers of Thladiantha dubia, will be noted in a subsequent section. See the paragraphs in the Fifth Section relating to the action of gravity.

base; frequently these are roots only, but in other cases the primordia of shoots appear as well, and there are not a few plants, such for example as Begonia, which are increased by leaf-cuttings. We can best bring these facts together under one general point of view if we assume with Sachs that the material which is devoted to the formation of the different organs is different. In the normal life of plants shoot-forming material would flow towards the vegetative points of the shoot, and root-forming material would pass to the root-system, and therefore, if there should be an interruption in the path of the stream, roots would of course appear at a root-pole and shoots at a shoot-pole, whilst in the leaves, seeing that the direction of the current of plastic material is always towards the shoot-axis, the new formations naturally appear at the base. Gardeners take care when they place the severed leaves of Begonia in moist sand to snick the thicker leaf-ribs, and then above each cut a bud appears.

The influence of gravity and light upon the phenomena of regeneration will be referred to in the Fifth Section. Here I will only further refer to one case which in a specially interesting way confirms the view that the place for the formation of new organs in regeneration is definite, and is primarily dependent upon the direction in which the plastic substance moves in the uninjured plant.

Many monocotyledonous plants seldom or never set seed because their vegetative propagative organs, for instance bulbs and corms under ground, exercise a stronger attraction upon the plastic material than do the ovules after fertilization has taken place [1]. We have examples of this in Lilium candidum, Lachenalia, and others. On flower-scapes of Lachenalia luteola [2], which have been severed from the parent plant, bulbils arise *near the base* because the current of plastic material was directed towards the base. In Hyacinthus orientalis, on the other hand, bulbils arise at the apex of severed flower-scapes and the seeds ripen normally because the current of plastic material flows to the ovules in which fertilization has taken place. The cause of the difference is not, as Vöchting has asserted, to be found in the limited or the unlimited growth.

The capacity of plants for artificial multiplication by cuttings is also related to the phenomena just briefly described. Different species behave differently in this respect; many are not able to produce new roots on detached twigs, and one and the same plant may even behave differently at different ages. The juvenile form of the Cupressineae, for example, roots very easily, the twigs of the older plants do so with difficulty. In

[1] See the Fifth Section.

[2] H. Lindemuth, Über Bildung von Bulbillen am Blütenschafte von Lachenalia luteola, Jacq., und Hyacinthus orientalis, Linn., in Ber. der deutsch. botan. Gesellsch., xiv. p. 247.

other cases, for example, in detached leaves of many plants[1], the formation of roots takes place but not the formation of shoots. I have obtained the formation of roots even upon the severed inflorescences of Klugia Notoniana and other Gesneraceae, which possessed no vegetative organs but only some small bract-leaves; a further development of these has however not yet taken place[2].

The propagative capacity of the different organs is very slight in some groups. In the ferns, for example, no case is known in which new plants have been formed from leaves detached from the parent, excepting in the case of the 'stipules' of Marattiaceae, in aposporous ferns and other abnormal instances, although shoots very often appear in this group upon the leaves which are still in connexion with the parent. In the Lycopodieae adventitious shoots are only known upon the first leaves of the embryo-plant of Lycopodium inundatum, the later leaves do not seem to be able to produce them.

The behaviour of the roots in the Pteridophyta is likewise variable. In some of them a formation of shoots takes place upon the uninjured roots[3], and such roots are, even when they are detached, specially suited for regeneration. The behaviour of Ophioglossum is interesting[4]:—A formation of shoots often takes place on the roots of uninjured plants very near their apices, and always upon very few roots of one plant, but if the apex of the plant be destroyed[5] then formation of shoots is much more copious, and particularly so from any severed root-tip a few centimetres long; the formation of shoots therefore takes place not at the shoot-pole but at the root-pole itself where evidently normal 'shoot-forming material' arises, but this material in the uninjured plant flows to the shoot itself. Any other portion of the root is also capable of regeneration.

It is interesting to note that the behaviour in regeneration of detached leaves is not in all circumstances the same. Sachs was the first to direct attention to this in the case of Begonia[6]. The adventitious shoots which arise upon leaves taken from plants which have arrived at their flowering period very soon produce flowers, but if the leaves be detached from plants which are not yet ripe for flowering then their adventitious

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[1] Many plants also form 'leaf-cuttings' without external influence. In this way adventitious shoots arise on the base of the fallen leaves of species of the aroid genus Zamioculcas and on the detached lower leaves of Nasturtium lacustre.

[2] This has now (1898) taken place in Tydaea hybrida; the inflorescences treated as cuttings have grown out into tubers.

[3] See Part II of this book.

[4] Poirault, Recherches anatomiques sur les cryptogames vasculaires, in Ann. d. Sc. Nat. sér. 7, xviii. p. 148.

[5] Similar relationships of correlation are known elsewhere, for example, in Populus tremula; many adventitious shoots are formed on the roots of felled trees of this species.

[6] Sachs, Physiologische Notizen 1, in Flora, 1892.

shoots will be much longer in flowering. I have repeated this experiment with Achimenes with a like result (see Fig. 19): leaves from the flower-region produced adventitious shoots which flowered much sooner than did those upon leaves which were taken from the basal region of the plant; the former produced usually only one to two leaf-pairs which had no flowers in their axils, the latter had always a greater number of pairs. Sachs concluded from his experiments that the flower-forming material was already in existence in the leaves of the plants which were

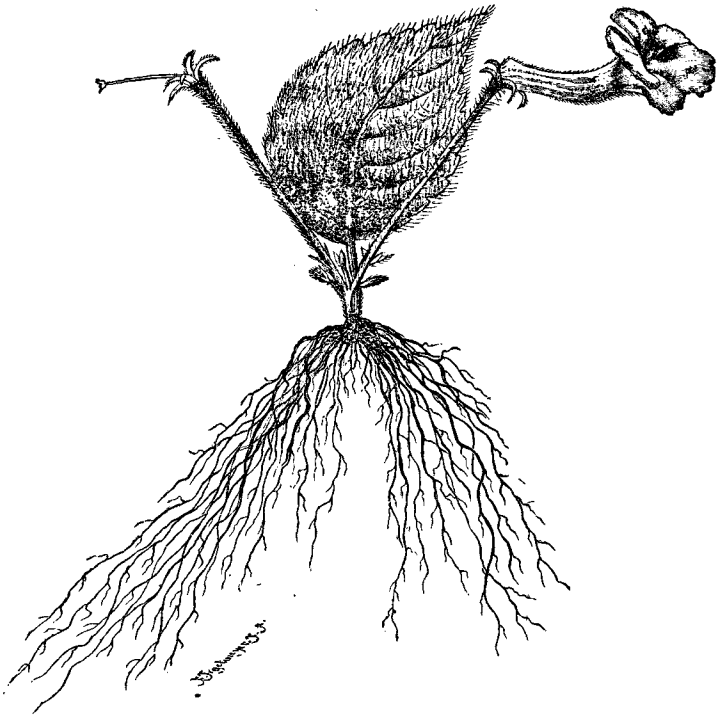

FIG. 19. Achimenes Haageana, a garden hybrid. A leaf of a plant ripe for flowering has been used as a leaf-cutting; at the basal end of the severed leaf-stalk an adventitious shoot has developed which has already reached the stage of bearing flowers.

ready to bloom. One could also say that the leaves of plants which are ripe for flowering will be generally poorer in plastic material, that the adventitious shoots which they produce would therefore from the beginning be 'enfeebled,' and we know empirically that the formation of flowers is favoured by lessening of the vegetative growth.

In mosses the propagative capacity is uncommonly great; one may almost say that nearly every cell of the vegetative body in mosses and liverworts, and in part also the cells of the sporogonium which is generally still capable of development, can give rise to a new plant. In the

regeneration of the mosses a new plant is not produced directly, but a *protonema* is first of all formed from which the plant arises, in the same way as the juvenile stage of the plant is developed from germination of the spore [1]. This is usually not the case in the liverworts. Even in the forms which develop a germ-tube from the spore in germination there is usually produced in the first instance upon detached leaves and other parts a *cell-mass*, and upon this the primordium of a new plant afterwards appears [2]. More accurate experimental examination of these differences is yet required. I believe that it is possible so to influence the leaves that in their regeneration the same phenomena will appear as are seen in the germination of the spore.

I may here cite a few particulars of the phenomena of propagation in Bryophyta.

In the foliose liverworts adventitious shoots arise, often in great numbers, upon severed leaves, but there is no preference shown for the base of the leaves as a point of origin. Here then is a difference between the leaves of liverworts and those of higher plants, for in the latter new formations always appear at the base, and I would attribute it to the fact that when the leaves of the liverworts, which consist of one layer of cells only, are cut off, the plastic material which was flowing to the shoot-axis collects at the base of the severed leaves in so small amount that they have not enough for the formation of adventitious shoots; plastic material can only be formed through the activity of assimilation in the severed leaves, and therefore regeneration remains in abeyance in the dark and also if the air be free of carbonic acid, because in both cases assimilation is impossible. There is no reason for a preference of the leaf-base in leaves in which plastic material is manufactured only after they have been severed, whilst in leaves which are rich in contents and possess a midrib, as is the case in some mosses, phenomena similar to those observed in the leaves of Spermaphyta may appear.

Amongst the thallose liverworts the behaviour of Marchantia has been thoroughly studied [3]. If a portion be cut out of a thallus by a transverse cut, adventitious shoots are only formed on its apex, that is to say, upon the side of it which was turned to the vegetative point of the uninjured plant; even small fragments of the thallus are quite capable of regeneration. With increase of age however the opposition between apex and base decreases, and if a quite old portion of a thallus be used for regenera-

[1] In Sphagnum, for example, a protonema-thread develops from severed pieces of shoot and it soon passes over into the flat protonema characteristic of the genus. I have not yet succeeded in obtaining regeneration from detached leaves of Sphagnum.

[2] See Schostakowitsch, Über die Reproduction und Regeneration bei den Lebermoosen, in Flora, lxxix (Ergänzungsbd., 1894); Goebel, Über Jugendformen von Pflanzen und deren künstliche Wiederhervorrufung, in Sitzungsber. der k. bayer. Akad. d. Wissensch., 1896.

[3] Vöchting, Über die Regeneration der Marchantien, in Pringsh. Jahrb. xvi (1865), p. 367.

tion adventitious shoots appear occasionally at the base also. Adventitious shoots may likewise arise on the base of the stalk of the gonophore if it is cut off from the thallus, and they may also spring from the walls of the gemmae-cups. Vöchting explains this by the limited or unlimited growth of the organs concerned, but I take this to be an altogether superficial cause—it would be superfluous to discuss his theoretical ideas —and it seems to me that we shall more likely find the cause in either the direction of movement of the plastic material or in the wound-stimulus. The behaviour of the thallus of the liverworts is thus very instructive. We may connect the appearance of adventitious shoots at the base of the stalk of the gonophore in Marchantia with the fact that elongation continues there longest, and consequently the plastic material flows thither from above; at the same time the polarity does not appear at all in others of the thallose liverworts, or not in the same amount, as in Marchantia [1]. The fact that in *old* portions of the thallus of Marchantia the polarity is obliterated gives special support to the explanation suggested here. The attractive influence of the vegetative point is very often limited and only extends to a certain distance from it. In young prothalli of Osmunda no adventitious shoots are found, but old ones which have reached a considerable length form them at their base which can no longer be influenced by the vegetative point (Fig. 20). A movement of material out of the posterior old part of a thallus of Marchantia towards its vegetative point cannot take place, or, if it does, only in a subordinate degree, and this determines its behaviour in regeneration.

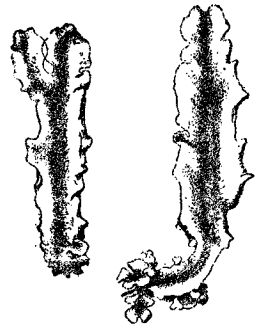

FIG. 20. Osmunda regalis. Prothalli. In the figure to the right many 'adventitious shoots' are shown at the base of the prothallus. Natural size.

Brefeld [2] has made known a number of similar phenomena amongst the Fungi.

The zygospore of Mucor Mucedo usually produces in germination *one* germ-tube, which, if the germination takes place in air, ends with a sporangium. If this tube be destroyed before the capacity of the spore for development is exhausted a second germ-tube grows out of the zygospore, and if the spore be submerged in water a third appears, and so on; naturally, owing to the reduced amount of material available, the sporangia on these tubes are successively smaller. The normal unbranched sporophore may also be induced to branch by injury inflicted upon it; if, for example, in the course of its elongation it be covered by

[1] See Schostakowitsch, l. c. on preceding page.

[2] Brefeld, Untersuchungen aus dem Gesammtgebiete der Mykologie.

a glass slide, or be attacked by parasitic fungi, or be influenced by other factors unfavourable to its growth.

The sclerotia of Coprinus stercorarius have a black cortex composed of firm compact tissue. If this be shaved off a new one is formed, and in the case of large sclerotia this may be repeated several times, reminding us very much of the formation of wound-cork in the higher plants. A large number of fructifications develop out of a sclerotium and of these one outstrips the others; if all be removed, new ones arise. If the pileus of a fructification be cut off, a new pileus does not arise from the cut surface, but hyphae sprout from this which proceed later to the formation of a typical fructification. Mycelium grows out from portions cut off from the fructification if they are brought into nutritive solutions; even the primordia of basidia can grow out again into mycelium. It is quite evident then that fungi behave in respect of regeneration in exactly the same way as do the higher plants; parts which have been removed are replaced only by 'embryonal' parts—to which of course belong spores, sclerotia, and like structures of which the contents consist essentially of 'germ-plasm,'—older parts, which are already differentiated, revert as in the higher plants to the 'embryonal' state, inasmuch as they grow out into hyphae from which a formation of organs can begin again. The pileus cut off from the fructification of a fungus, or the sporangium removed from the germ-tube of Mucor, can no more be directly regenerated than can a detached flower or a portion of a leaf—there is always a vegetative hyphal stage interposed. The fact that a new fructification is formed quicker after the removal of the pileus of a previous fructification than under other circumstances reminds us of the phenomena which have been cited in Begonia and Achimenes; and it shows that the 'disposition' which the parts of the plants have acquired is concerned in the regeneration.

The behaviour of the severed leaves of mosses leads to a similar reflexion. Whilst the leaves of plants which are not in fructification produce easily and quickly new plants—indeed these arise from the protonema formed from the leaves quicker than they do on the protonema formed in spore-germination—in plants which are in fructification such a formation of new plants, according to my experience, does not happen or only occurs slowly after a long time; and this is so because all the plastic material has flowed out from the leaves to the sporogonia, and perhaps also the plasmic body of the cells has already undergone some not yet visible changes.

Shoots which have been separated from plants to serve as cuttings retain in general the peculiarities which they possessed. In a fir or a spruce a plagiotropous dorsiventral lateral shoot may grow erect after removal of the terminal chief shoot, and can therefore become radial, and one

would naturally expect that a lateral shoot removed from the shoot-system and planted vertically and which rooted would behave similarly. We must however bear in mind that in the cutting nutritive relationships obtain other than those occurring in the lateral shoot attached to the tree from which the chief shoot has been removed. The whole root-system of the plant, and all the existing food-material in it, stands at the disposal of the attached lateral shoot, which becomes the chief shoot through stronger nutrition. The rooting of cuttings of Coniferae is relatively feeble, and in proportion to this stands the nutritive activity which cannot overcome peculiarities imprinted on the twig, that is to say, its disposition; as a consequence branch-cuttings of the fir form chief axes only with difficulty. I have seen the leaf-like distichously-leaved branches of Phyllanthus lathyroides grow up as cuttings to many times the length which they reach on the parent plant; they were not radial, although at their base radial shoots developed.

V.

CONCRESCENCE AND ARREST.

The investigation of the formation of organs at the vegetative point frequently does not suffice for the recognition of homologies, because these are often concealed through occurrences which can be elucidated only by comparison with other forms.

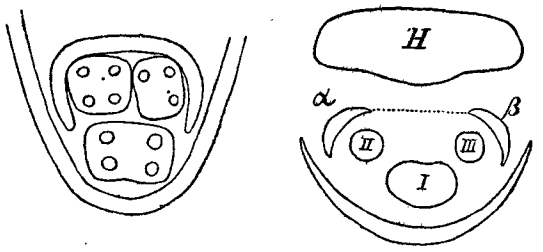

FIG. 21. Scirpodendron costatum. Figure to left: transverse section of a three-flowered spikelet. Figure to right: diagram of same. *H* axis of inflorescence with bract opposite. *I* primary flower in axil of bract, α and β, prophylls in axils of which arise secondary flowers *II* and *III*.

Let us assume, for example, that the flower-organs which are represented to the left of Fig. 21 [1] belonged to an isolated monocotyledonous plant whose stamens occurred only in the number and with the arrangement shown. Every one would say we have here an axillary male flower with only one perianth-leaf; as a matter of fact however there are three male flowers, each of them being reduced to a single stamen, and the perianth-like leaf is not

[1] See Goebel, Über den Bau der Ährchen und Blüten einiger javanischen Cyperaceen, in Ann. du Jardin Bot. de Buitenzorg, vii.

one at all but is the prophyll of the first flower, and is made up of two concrescent leaves in the axil of each of which stands a flower composed of a single stamen.

We are here forced to consider the formation of the flower as the result of an arrest of the whole perianth, of five stamens, and of the gynaeceum of the typical flower of Cyperaceae, accompanied by a concrescence of the two prophylls. Morphology which seeks to fathom homologies constructs for itself an arbitrary starting-point, which may either coincide with some living form, or may be an ideal type, and all the relatives of one series are represented as deviations from this 'type.' The deviations commonly result from either an arrest, a concrescence, or a transformation, and these changes often stand in the clearest relationship to the environment, or they are conditioned by internal relationships of the organs to one another. Three methods are available to organography for the recognition of the changes which have taken place in the formation of organs — comparison with allied forms, history of development, and experiment. I have already dwelt upon the importance of Experimental Organography, and have cited some confirmative illustrations when speaking of the doctrine of metamorphosis in an earlier chapter. It is one of the youngest branches of the study of organs, and for it one may presage an important future, and therefore in a subsequent chapter I will record the results which have up to now been obtained. Of course experimental organography shades into physiology, but, as I have already briefly pointed out, the separation of morphology from physiology is a purely formal matter, and I include here within the province of organography all those lines of investigation which touch upon the formation of the organs of plants, no matter what methods they employ.

The notions of concrescence and of arrest have been applied at different times in different senses, and it will not therefore be superfluous if I examine them in some detail. Individual illustrations will be given in the course of the second part of this book.

CONCRESCENCE.

The expression 'concrescence' is used partly in a literal, partly in a comparative sense, that is to say, it has been understood to convey not only the fact that organs, originally separate from one another, unite by their free parts, but also that many organs, which in certain plants are found free and independent, are in others united with one another, although this union is not brought about in the course of their development.

One of the best-known examples is afforded by the corolla of the Gamopetalae, which is usually described as composed of concrescent

leaves. In reality what happens here is that a number of free primordia of leaves are formed, but these are soon raised up upon a common circular base. We may consider this ring as made up of the basal parts of the leaf-primordia which from the beginning, or 'congenitally,' are united with one another. In speaking later of the formation of the flower I shall revert to this point; meanwhile a few examples illustrating the existence of an *actual* concrescence may be given.

In the first place it is to be noted that the earlier the concrescence has taken place the less evidence of it is there in the mature condition. The false septum of the fruit of the Cruciferae, for example, is composed of two portions which have united with one another; the junction of the cells takes place so early however that this is not visible usually in the mature condition. The same is the case in the union of many carpels, in the corolla of Ceropegia and other plants. A temporary or permanent concrescence by sutural union occurs between the leaves of the perianth in many cases of 'valvate' vernation[1]. Either the epidermal cells of adjacent leaves which touch one another grow in tooth-like between one another

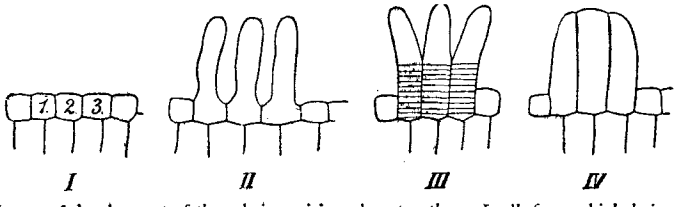

FIG. 22. Scheme of development of three hairs arising close together. *I* cells from which hairs arise, 1, 2, 3 *II* free development; *III* partial concrescence; *IV* complete concrescence.

and then we can speak of a 'cell-suture,' or the toothing involves only the ribs and prominences of the cuticle and then we speak of a 'cuticular suture.' In the latter case the concrescence takes place only after the formation of the cuticle and is therefore different from the former; and it may be afterwards dissolved by partial resorption, as in the staminal tube of Lobelia, according to Reiche.

The instances I have mentioned are indeed of biological interest, yet they have not the importance which attaches to *congenital* concrescence—a condition involving, as I have stated, altogether different incidents.

Let us take a sample case, illustrated in Fig. 22. The three adjacent epidermal cells, 1, 2, 3, represented in *I*, are about to develop into hairs. They may do so independently as at *II*. In an allied plant they grow from the beginning as a single cell-body. This may be designated congenital concrescence of single cells, an expression which has primarily

[1] See Reiche, Über nachträgliche Verbindungen frei angelegter Pflanzenorgane, in Flora, 1891, p. 435; Raciborski, Die Schutzvorrichtungen der Blütenknospen, in Flora, lxxxi (Erg.-Bd. 1895), p. 151.

a purely comparative meaning, that is to say, it is merely another way of stating the fact that the cells in the first plant have not coalesced with one another; and it is only of significance if it gives probability to the congenitally concrescent body having had its phylogenetic origin in the free hairs. A support to this declaration would be obtained if a plant were known in which the hairs occurred as is shown at *III* in the figure, where they are only combined in their lower part, that which is shaded in the diagram. Such a condition might be reached in two ways—either the hairs might grow out at first free and then be raised up by elongation of their common basal part, or at the outset a cell-mass might arise, like that at *IV*, corresponding with the shaded part of *III*, and upon its top the three free cells might then shoot out. We find in the origin of the gamopetalous corolla examples of both these methods.

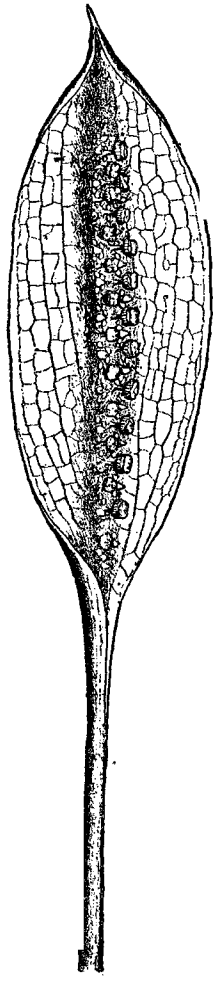

FIG. 23. Spathiphyllum platyspatha. The unilateral inflorescence viewed from above somewhat obliquely. The spadix is 'concrescent' with the spathe; there are two rows of staminate flowers, and between them the pistillate flowers.

A phenomenon which corresponds exactly with the concrescence of hairs as just described is observable in the hair-roots of many Florideae and of some liverworts. In most species of these groups solitary hair-roots are known; in some of them cell-masses occur which may be designated 'congenitally concrescent' root-hair tufts; such are found in Polyzonia jungermannioides among the Florideae [1].

In all cases where a congenital concrescence is assumed upon comparative grounds historical developmental proof must show *how* it really takes place. Both methods of investigation must mutually complete and correct one another. The inferior ovary, for example, was from the historical developmental side very often considered as formed of the cup-like torus; the carpels would then be represented by the styles only. Comparative study however led to the conclusion that in the inferior ovaries the carpels take a share in the formation of the ovary, and that from them the ovules arise; and this without giving thereby a clear explanation of the process itself. The accurate pursuit of the history of development has shown, in all cases

[1] With regard to the liverworts, see my 'Pflanzenbiologische Schilderungen,' i. p. 161, fig. 66.

which have been examined up to the present, that both these views of the ovary are in a certain sense right, although they must be combined together. Upon this subject more will be said in the special part of this book.

I may here by means of Figures 23 and 24 shortly explain another example. The spadix of the Aroideae is invested by a bract, commonly designated a spathe, which arises below it. Spathiphyllum platyspatha is peculiar in having the spadix concrescent throughout its length with the spathe, and the flowers arise only upon the free slightly-projecting side of the spadix opposite to that which is concrescent with the spathe. A transverse section through the spadix (Fig. 24, *III*) awakens the suspicion that the flowers spring out of the upper side of the spathe which by its inturned edges surrounds in a protecting manner the inflorescence. The history of development shows however that the spathe is laid down

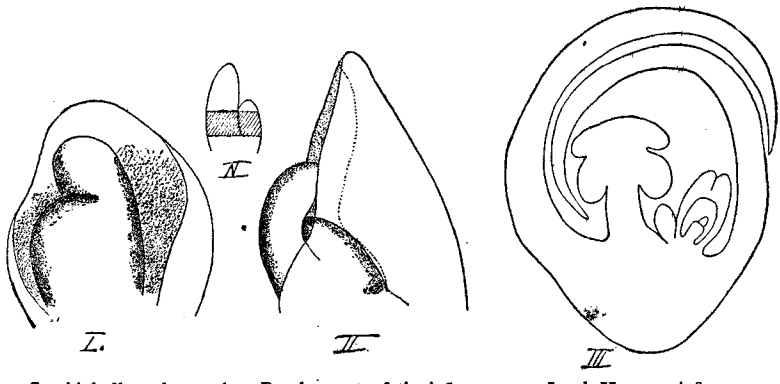

FIG. 24. Spathiphyllum platyspatha. Development of the inflorescence. *I* and *II* young inflorescences upon which is seen the primordium of the spathe sprouting laterally beneath the vegetative point of the inflorescence. The leaf opposite the inflorescence will become a scale-leaf in the axil of which a continuation-shoot will arise. *III* transverse section through a young inflorescence. *IV* diagrammatic figure to illustrate the 'concrescence.'

quite normally below the apex of the spadix (Fig. 24, *I* and *II*), but, instead of the portion of the spadix *above* the point of origin of the spathe growing, as is usual, and becoming covered with flowers, the zone of it which is united to the spathe develops greatly (this zone is shaded in the diagram, Fig. 24, *IV*) and attains maturity, consisting outwards of the inflorescence axis (in Fig. 24, *IV*, the portion to the right), and inwards of the base of the spathe; and thus by the *united growth* of the shoot-axis and the leaf-insertion the wonderful structure from which we started is produced. Other species of Spathiphyllum show this concrescence in much less degree and only at the base of the spadix. We do not know the biological relationships with which the peculiar change in the course of development in Spathiphyllum platyspatha has been connected.

ARREST[1].

The more elaborate the differentiation a plant exhibits the more common is the appearance which we designate as arrest. In Thallophyta it appears relatively seldomer than in the higher plants, and in the latter it is more common in the region of the flower than in the vegetative region, in correspondence with the higher differentiation exhibited there. We leave of course out of consideration in this all the cases in which an organ is retarded in its development by unfavourable *external* influences; here we have only to do with forms of arrest which are due to inner causes. The following general statements may be made regarding these:—

1. KINDS AND MANNER OF ARREST.

Arrest is brought about by the primordium of an organ not passing through its complete course of development but remaining stationary at an earlier or later stage. In some cases the primordium of the organ can be proved to have a developmental existence—it is *aborted*. In numerous other cases however the first laying down of the primordium does not take place—it is *suppressed*; arrest can then only be determined by *comparison* with other forms. There is however no sharp line between *abortion* and *suppression*; one and the same organ may be sometimes aborted, sometimes suppressed, in the same plant, and this is again only a special illustration of the general rule that organs liable to arrest show great variation in the degree of development at which they arrive. The following are some examples:—

The spikelets of species of Setaria, Pennisetum, and other grasses are surrounded by an envelope of bristles. The history of development shows that these bristles are unquestionably branches of the inflorescence on which indeed the rudiments of flowers are sometimes found. But in most of the many cases I have investigated [2] I could find no trace of the formation of flowers on the bristles, and this circumstance shows that a sharp distinction between abortion and the suppression of the development of shoots cannot be drawn. If we find upon a bristle of Setaria in one case an almost complete spikelet, in another only a trace of the glumes, and in a third no rudiment at all of a spikelet, these three stages must be regarded as only different in degree from one another. Similar examples may be drawn from the formation of leaves. Schmitz states[3]

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[1] [The term *Arrest* is here used as the equivalent of the German 'Verkümmerung' in its widest application and as including *Abortion* or partial arrest ('Verkümmerung' in its narrower sense, or 'Abortus'), and *Suppression* or complete arrest ('Nichtanlegung'). The latter terms are used in the same sense as they are by Masters in his 'Teratology.']

[2] Goebel, Beitr. zur Entwicklungsgeschichte einiger Inflorescenzen, in Pringsh. Jahrb. xiv.

[3] Schmitz, Die Blütenentwicklung der Piperaceen, in Hanstein, Botan. Abhandlungen, ii. p. 37.

that in Artanthe jamaicensis, one of the Piperaceae, only the posterior stamen of the inner staminal whorl is formed, but it is larger than the three stamens of the outer whorl; in some flowers however this posterior stamen only appears as a protuberance and does not reach complete development and is apparently absent; sometimes the first laying down of such a protuberance is suppressed even to the first cell-divisions, and therefore the formation of such a member can only be concluded from other circumstances [1].

It is not always easy to separate arrested organs from those which are *transformed* and from those which experience only a *temporary retardation* of their development. The leaves, for example, on the rapidly growing shoot-axes of many climbing plants remain at first in an undeveloped condition, and are either thrown off in this state or resume later their development. The 'resting buds' of many trees become arrested when they are not called upon to sprout through an injury to the tree.

The examples which have been already briefly referred to show that the arrest may take place earlier or later in one and the same organ, and consequently the construction of arrested organs varies in an extraordinary degree. Examples from the vegetative region as well as from the flower-region can be easily found. The lowermost glume of the spikelet of Lolium is in most cases suppressed, but in Lolium temulentum its presence can always be proved in development, and it often reaches such a size that it is visible to the naked eye. The bracts of the flowers of Cruciferae are usually suppressed, but sometimes they appear. Arrested stamens show all intermediate stages from the normal structure of the anther to an unsegmented papilla [2]. It is quite characteristic of many flowers with greatly developed corollas that the stamens experience a very early retardation of their growth, which does not occur in so great a degree in the carpels which follow them; the ray-florets of many Compositae supply illustrations. Carpels and ovules also show all stages of arrest. Organs in a condition of arrest usually appear somewhat later than their position would warrant, and if it should happen that there is no trace of the organs at all then the very spot on which they ought to stand may disappear. Thus, for example, the flower of Labiatae is typically pentamerous, but the development, from the formation of the corolla inwards, is quite that of a tetramery.

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[1] Schmitz has introduced the term 'Ablasty' for the suppression of all trace of an organ in contra-distinction to 'Abortus.' As has been stated in the text, there is no essential difference between the two processes; the assumption that an organ has disappeared can only be determined by comparative investigation. The circumstance that in such comparisons mistakes are sometimes made cannot be regarded as an obstacle. [See note 1 on preceding page. 'Ablasty' is the equivalent of *Suppression*.]

[2] Familler, Biogenetische Untersuchungen, in Flora, 1896, p. 133.

2. CAUSES OF ARREST.

We have here to consider two sets of causes which may however come into consideration together:—

(1) The arrest may take place through the influence of other parts of the same plant, that is to say, directly through correlation.

(2) The arrest may be a consequence of the loss of function of the organ, and the reduction of the organ may be caused either directly by its loss of function, or only indirectly, inasmuch as an arrest of useless organs will benefit the others, at any rate there will be less demand upon the plastic material. The loss of function takes place in many cases by another organ taking over the function in question, for example, the shoot-axis may take on the function of assimilation which commonly is the work of the leaf.

(1) *Arrest through correlation.* Numerous examples may be given of this, but as these will be specially dealt with in the chapters treating of the phenomena of correlation a brief reference is all that is necessary here.

The prothalli of ferns and the protonemata of mosses, with the exception of that in Ephemerum, die off when a young plant has arisen upon them and takes off to itself the plastic material. In the ovary of the oak one only of the six ovules develops, in the case of the lime one only of ten ovules develops, and supplants all the others. The upper flowers of the many-flowered inflorescences in Boragineae, Oenothera, and other like plants, are arrested if the lower flowers set seed. The buds at the base of the annual shoots of most broad-leaved trees are quite as capable of development as the others, but owing to their position they are arrested and remain as 'resting buds,' and only under definite external conditions elongate into shoots. Many other instances occur.

(2) *Arrest due to loss of function.* It is not always easy to prove *why* the loss of function takes place; that it does occur is very evident in most instances. A number of cases taken from the vegetative region will be found in the chapter upon relationships of symmetry, and I will only refer to a few here.

In the inflorescence of Lolium, which was referred to above, one of the two glumes which in grasses usually invest the spikelet is suppressed in the lateral spikelet, but the terminal spikelet possesses both of them. This happens in the terminal spikelet because it lies free and requires a protection upon every side, but the lateral ones lie in a depression of the axis of inflorescence which covers them on one side whilst the other side is protected by the lower glume; the upper glume on the side next the axis of inflorescence is here quite superfluous and is consequently suppressed. The bracts of many flowers show similar phenomena. Where the flowers stand closely grouped together their

protection by bracts can be dispensed with, especially when, as in the Compositae, there is an involucre serving as a common protective apparatus to the whole of the flowers; the bracts in such cases are arrested. Plants which have umbels are particularly instructive in this respect[1]. On the umbels of the first and second order we find commonly, although not always, the bracts of the outer branches of the inflorescence or of the flowers; they form the 'involucre' or the 'involucel' of descriptive botany. So far as I have investigated living Umbelliferae with reference to this point I find that the involucre is the more likely to be present the less protection otherwise the inflorescence has. If the inflorescences remain for a long time within the massive vaginæ of the leaves in the axil of which they arise the involucre and involucel are wanting; if that is not the case then these have a function to perform and are retained for protection. In illustration of this we may compare Angelica sylvestris with Daucus Carota. Of course such a relationship cannot be stated as a universal rule because other relationships have to be taken into account.

The arrest of the corolla in cleistogamous flowers is a characteristic example of the effect of loss of function, inasmuch as the condition here is a direct consequence in many plants of external influences[2] and is not a reduction ensuing through a gradual loss of function of the corolla in the course of generations.

Although at present we are not able to find in the life-relationships of plants satisfactory reasons for the arrests that are observable, yet more accurate investigations may yet enable us to determine these. In the family of the Ranunculaceae, for example, we have a very gradual gradation from the carpels of the Helleboreae which bear many ovules to those of the Ranunculeae which produce only one; in the Anemoneae and Clematideae the existence of the arrested ovules can be easily proved by a study of the development. When now the facts are examined from the biological standpoint it will be seen that the Helleboreae have only few carpels in the flowers, whilst the Ranunculeae and Anemoneae have many; in other words, diminution of the number of seeds in these plants lies at the bottom of the whole arrest, for in this way those that are developed will be better nourished, and this result is attained either by the reduction in the number of the carpels or of the ovules. That this reduction takes place can be proved in the development of the Anemoneae and the Clematideae, but not in the Ranunculeae.

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[1] The young inflorescences of the Cruciferae conform in every respect with young umbels, the internodes of the axis of inflorescence only elongate later; it is therefore not surprising that the bracts have been suppressed.

[2] See the Fifth Section.

3. MORPHOLOGICAL IMPORTANCE OF ARRESTED ORGANS.

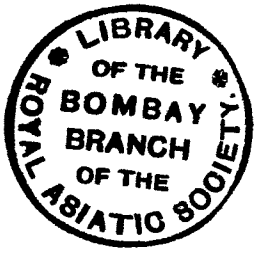
The morphological importance of arrested organs lies in the fact that they often supply the clue by which affinities with allied plants can be ascertained, and phylogenetic morphology is accustomed to interpret arrested organs as vestiges of ancestral structures. It is probable, for example, that the flowers of Salvia, which possess at the present day two complete and two arrested stamens, took origin from a form which like other Labiatae possessed four developed stamens.

We must however guard against considering *all* arrested organs as being descended from organs which were developed in the ancestors of the existing forms. Such a view would be a mere chimaera in the case of the regularly arrested flowers of many inflorescences. The assumption is much more probable in their case, as I have already endeavoured to prove in connexion with the inflorescences of grasses[1], that the plastic material which is present in an inflorescence suffices indeed for the laying down but not for the unfolding of a great number of organs, and this may have been the case from the first in any of our existing forms. It is indeed a quite general rule that many more primordia of organs are formed than become functional, and this failure of function is brought about, as in the cases that have just been mentioned, either by an early arrest of the primordia of the organs or by the withering of the completely formed organs.

Most of our phylogenetic series are reduction-series, that is to say, are those in which the changes are brought about by arrest. There is a simple psychological explanation of this. If we have a definite 'type' we obtain through it a fixed starting-point for our comparison. But this is wanting when our comparisons deal with an ascending and not a descending series. It is specially necessary to refer to this because arrests have frequently been assumed upon the *subjective* grounds above indicated without definite proof of them being existent. Thus, for example, Celakovsky has lately traced all of the flowers of the Gymnospermae from hermaphrodite flowers, and chiefly because in Welwitschia a rudimentary ovule is present in the male flower. This is a pure construction of the imagination, and the assumption that 'function-less structures are always only the vestiges of former completely formed ones which functioned as normal organs' is no more, nor generally, valid, as will be concluded from what I have said above, and before now elsewhere, than would be the assumption that the ancestors of men were hermaphrodite because man possesses rudimentary mammae and

[1] Goebel, Beitr. zur Entwicklungsgeschichte einiger Inflorescenzen, in Pringsh. Jahrb. xiv.

a rudiment of a uterus which early degenerate. Arrested organs may be such as generally in the existing species (or in its one sex) *never* reached complete development; it is only our synthetic necessity which forces us always to the assumption of reduction-series, of which, however, many can only claim to be fictions, imparting the aesthetic pleasure of bringing a series of facts into connexion with one another.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SECOND SECTION

RELATIONSHIPS OF SYMMETRY

RELATIONSHIPS OF SYMMETRY[1]

I.

INTRODUCTION.

By the expression 'relationships of symmetry' we understand here the general relationships in space of the configuration of plants. The plant-body is seldom developed equally in all directions of space, although this is the case or appears to be so in the monergic spherical cells of Eremosphaera; the construction is usually different in different directions. The investigation of the relationships of symmetry is of great importance, because they stand in the closest connexion with life-phenomena and are also of considerable significance for the formation of a critical estimate of the whole construction of the plant. The 'spiral theory,' which for so many years dominated morphology and frequently led into blind alleys, was founded essentially upon an incorrect generalization regarding the relationships of symmetry of orthotropous shoots of the higher plants.

We must first of all recall here, what was explained in the preceding section, that most plants and parts of plants show a *polar* construction, an opposition between *apex* and *base*—an opposition which is seen indeed in many cell-colonies, but which is only sharply marked when a vegetative point comes into existence, because with its appearance the polarity is impressed on parts from their beginning. We have seen that its phenomena are well marked in the regeneration of many parts of plants. In normal life the different construction of an apical and a basal region is very conspicuous, particularly in trees and shrubs. We notice in these

[1] See Von Mohl, Über die Symmetrieverhältnisse der Pflanzen, Vermischte Schriften, 1845; Herbert Spencer, Principles of Biology, ii.; Sachs, Lehrbuch der Botanik; Id. Über orthotrope und plagiotrope Pflanzenteile, Arb. d. bot. Instituts in Würzburg, ii. p. 226; Id., Gesammelte Abhandlungen, ii.; Goebel, Über die Verzweigung dorsiventraler Sprosse, in Arb. des bot. Instituts in Würzburg, ii. p. 353; Id., Vergleichende Entwicklungsgeschichte der Pflanzenorgane, p. 141.

plants that the lateral twigs are the more developed the nearer they lie to the point of the annual shoot, an arrangement which appears specially to favour a regular expansion of the woody skeleton. A pine-tree has no lateral shoots at the base of its annual shoot; higher up spur-shoots appear upon this, but only at the summit do the long shoots arise in a false whorl; there is produced in this way upon the chief shoot itself a tiered structure whereby the branches do not cover one another, whilst on the lateral shoots the branches of higher order always arise further from the chief stem, and so carry the organs of assimilation to the periphery where they will find the most favourable illumination. Many broad-leaved trees behave in a similar manner, only a more gradual gradation takes place in them, and the buds which are found at the base of the annual shoot are frequently destined to act as resting buds which only unfold in the event of injuries to the plant making a call upon them.

Apex and base of a plant or of its part may be connected by an imaginary line which we designate the *long axis*.

Leaving out of consideration a few exceptional cases, we may distinguish in the arrangement of the lateral organs and the construction of the organs themselves three kinds of cases:—

1. *Radial construction.* This it is when an organ shows no differentiation into an anterior and a posterior side, nor into a right and a left side, but is organized about the long axis in every radius of the transverse section in nearly the same manner[1].

2. *Bisymmetric* or *bilateral organs.* We understand, by these, organs which have an anterior and a posterior side, and a right and a left side, which are respectively like to one another. The distichously-leaved shoot of Schistostega (Fig. 25) and Fissidens, and the pinnate thallus of Bryopsis, are, for example, bilateral. In Schistostega the bilateral configuration has moreover arisen in the course of development out of a radial one. The leaves, which in the mature shoot stand in two rows attached throughout their length to the stem, are inserted transversely on the vegetative point and distributed around the shoot-axis (Fig. 26). Opuntia shows this transition even more simply: the radial shoot-axis becomes flattened on two opposite sides and thus develops into a bilateral structure. How near radial structure stands to bilateral structure we also see in many marine Algae, of which the thallus, fixed only at its base, floats freely in the water and is sometimes flat, that is bilateral,

[1] This form of construction was originally designated the 'concentric' by E. Meyer in Linnaea, vii. p. 149—a term which has rightly been passed over. It was especially unsuited to the radial distribution of lateral organs. Unfortunately A. Braun introduced a special terminology for the flower; radial flowers he designated 'actinomorphous,' dorsiventral he termed 'zygomorphous.' These clumsy names are in my opinion altogether superfluous.

sometimes cylindric, that is radial. Many leaves also, like those of Iris, are in the main bilateral.

3. *Dorsiventral organs.* These, as the name indicates, have a dorsal side and a ventral side which differ one from the other. The two lateral surfaces, the flanks, may be like one another or they may be different. The latter is the case, for example, in the inflorescences of Vicia Cracca which have flowers set in oblique lines along only one side.

These categories define the most frequent cases only; that they pass readily into one another has already been shown in the case of Schistostega. Just as an organ laid down as a radial one may become bilateral, so also a bilateral or radial one may become dorsiventral, and many examples of this will be given in the course of the following pages.

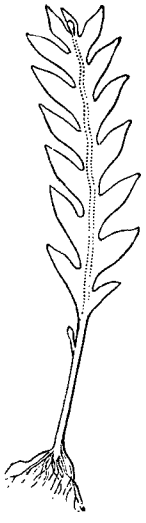

FIG. 25. Schistostega osmundacea. Distichously-leaved plant illustrating bilateral construction. Magnified.

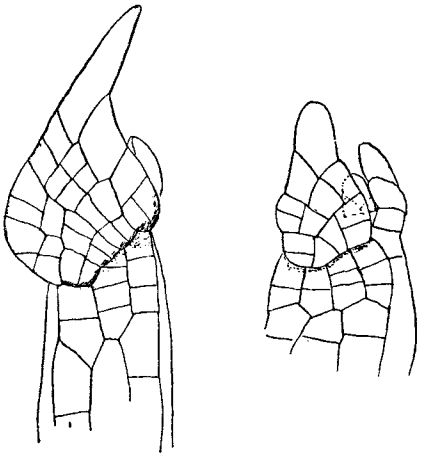

FIG. 26. Schistostega osmundacea. Two shoot-apices seen from outside. The primarily transverse insertion of the leaf is displaced towards the long axis of the shoot.

I must in the next place shortly mention relationships which exist between symmetry and direction of the organ.

Sachs has divided the organs of plants into the orthotropous and the plagiotropous. An organ is orthotropous if, under usual conditions of life, it grows vertically upwards or downwards when it is illuminated equally on all sides; it is plagiotropous if, under such conditions, it assumes an oblique direction to the horizontal plane. The external and internal influences which take a share in this we shall not here consider, but it is important for organography to note that orthotropous organs are almost always radial or bilateral; plagiotropous ones, on the other hand, are commonly dorsiventral, seldomer

bilateral as in the bilateral shoots of Schistostega and Fissidens. Familiar illustrations of this are the orthotropous chief axes of herbaceous plants of which the radial configuration is visible without further investigation, and the ordinary plagiotropous leaves in which dorsiventral structure shows itself in the differences between upper and under surface, whilst the radially constructed leaves of Juncus, which are commonly, and indeed in part perversely, called 'sterile haulms,' are orthotropous just as are the bilateral leaves of Iris and other plants.

FIG. 27. Hypnum (Hylocomium) splendens. Tiered growth. The shoot of each year at first orthotropous becomes plagiotropous and branches in one plane. Natural size.

The seldom occurrence of bilaterality in plagiotropous organs[1] stands in connexion with the fact that most of them, especially under the influence of one-sided illumination, have become dorsiventral. We consider that in most cases the plagiotropous direction, caused by external and internal factors, is the primary one, the dorsiventral construction is secondary. We may also say that the radial character of most subterranean plagiotropous organs is connected with the fact that light has a special significance in the determination of dorsiventrality. Once an organ has imprinted upon it a dorsiventral character it reacts towards outer influences differently from a radial one.

The relationships vary very much in details. One and the same organ may in different stages of its development be orthotropous and then plagiotropous, or, in consequence of the different influences of external stimuli, it may behave either as an orthotropous or a plagiotropous structure, or, because of relationships of *correlation* especially, plagiotropous organs may pass over into the orthotropous condition; we find also not infrequently that the vegetative shoots are plagiotropous whilst those of propagation are orthotropous[2]; this occurs, for example,

[1] See the examples cited above.

[2] I have before now referred to the fact that the shoots of many dicotyledonous plants (Gentiana asclepiadea, species of Lonicera), which in free illumination on every side are orthotropous, become plagiotropous in restricted unilateral illumination because this gives them a better means of utilizing the light. See Beitr. zur Morphologie und Physiologie des Blattes, in Botan. Zeitung, 1880, p. 753.

in Mnium undulatum (Figs. 28 and 29). A beautiful example of the transition first mentioned is afforded by the growth of Hypnum splendens. This moss, growing in the shade of woods, possesses (see Fig. 27) distichously-branched shoots which are expanded at right angles to the incident light and resemble very closely pinnate leaves. Each of these plagiotropous shoot-systems bears small leaves and is only capable of vegetation during one vegetative period. At the beginning of the next period there develops near its base a strong orthotropous lateral shoot which remains unbranched; it soon becomes plagiotropous, branches distichously, and spreads out in a plane at right angles to rays of incident light. As the old dying-off generations of shoots remain for some little time there is developed a tiered construction which prevents the

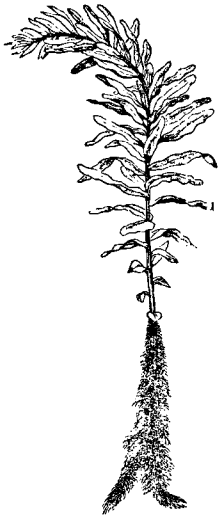

FIG. 28. Mnium undulatum. Vegetative shoot. It is at first orthotropous and afterwards plagiotropous. Natural size.

FIG. 29. Mnium undulatum. Orthotropous shoot ending in a group of antheridia girt by a rosette of leaves; below this three shoots, plagiotropous from the outset, arise on the orthotropous chief shoot. Natural size.

new shoot-generation from being buried in the detritus of the soil of the wood.

To a certain extent the behaviour of the pine is analogous; it possesses orthotropous chief shoots and plagiotropous lateral shoots, but the outgrowing tips of the new lateral shoots in spring are at first orthotropous and it is only later, evidently through correlation and under the influence of the chief shoot, that they become plagiotropous.

Many trees possess, at least in their later years of life, exclusively plagiotropous shoots, although the plant exhibits the configuration of an orthotropous chief stem; this is however produced by the concatenation

of plagiotropous shoot-generations. It is thus in the beech, the lime, and the elm. Orthotropous shoots are formed in these trees only in the young condition in germination, and they differ therefore in configuration from the plagiotropous ones which appear later. The latter are distichously-leaved and dorsiventral. The seedlings of the beech[1] are orthotropous, the first two leaves being placed at right angles to the cotyledons, and with them the seedling plant usually closes its growth for the season; occasionally however a third leaf appears over one of the cotyledons. The terminal bud of the first annual shoot is however already dorsiventral[2]. Ulmus possesses in its first year decussating whorls of foliage-leaves, alternate distichous phyllotaxy appears only in its second year and on the first lateral shoots of the axis of the seedling which has limited growth. The seedlings of the lime are radial with a two-fifths phyllotaxy. All these trees produce later *dorsiventral* distichously-leaved plagiotropous shoots only, nevertheless there is built up a stem with a *radial* crown,

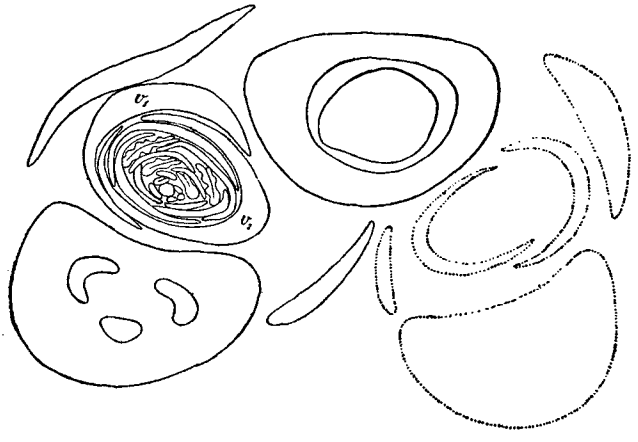

FIG. 30. Transverse section of a twig of a lime-tree. One lateral bud with distichous leaves has been cut through; its plane of symmetry does not coincide with that of the mother-shoot.

such as exists in other trees from the beginning. This comes about in this way: the planes of symmetry of the generations of shoots which follow one upon the other do not coincide (see the diagram in Fig. 30); in the shoots then which grow in the main erect, the stem, composed as it is of different generations, will have a radial construction, whilst on the shoots growing more horizontally the plane of symmetry of their dis-

[1] According to Döll, Flora von Baden, p. 537, the phyllotaxy of the seedling plant of Fagus sylvatica and of Carpinus Betulus, as well as of Ulmus, is partly spiral, partly decussate. The seedlings of Ulmus which I examined, either U. campestris or U. effusa, had altogether decussate phyllotaxy and the leaves were not asymmetric as they are on the later plagiotropous shoots.

[2] See Kolderup-Rosenvinge, Undersøgelser over ydre Faktorers Indflydelse paa organdannelsen hos Planterne, in Vidensk. Medd. Naturh. Foren. i Kjöbenhavn, 1888.

tichously-leaved lateral shoots becomes vertical through torsion of the internodes, and thus these horizontal lateral branches exhibit a form which is like that of a many-times pinnate leaf possessing a dorsiventral construction[1].

The intensity and the direction of the light on the one hand, and on the other hand the relationships of correlation, play an important part in bringing about the difference in direction of the several shoot-systems of such trees as are built up out of plagiotropous shoots. The chief shoots of the beech, for example, growing in the open are erect, in feebler illumination, for instance in dense woods, they become almost horizontal. Further investigation is required to determine the extent to which the lateral shoots may be induced through the influence of the more erect-growing chief shoot to assume a greater inclination to the horizontal plane.

Exceptional cases are not unknown. Vicia Faba, for example, is a leguminous plant which, like many others of its order, is dorsiventral in its branching[2], its shoots are however orthotropous. Still in the largest number of cases the rule above mentioned holds good.

It may be of interest to quote from the lower plants some illustrations of the relationship between symmetry and direction.

In lichens the difference between dorsiventral thalli which are usually pressed close to their substratum, as in the 'foliose' forms, and the radially constructed ones which usually stand erect or hang pendant, as in the 'fruticulose' forms, is very clear, and the transition from dorsiventral to radial organs which takes place in many lichens is specially interesting[3]. Such a transition may take place in three distinct ways:—

1. By convolution of a dorsiventral thallus or portion of a thallus.
2. By formation of orthotropous vegetative outgrowths on a dorsiventral thallus.
3. By development of the stalk of the fructification; this becomes very conspicuous and leads to the production of peculiar vegetative organs if at a later period of development the formation of the sporiferous portion is reduced or suppressed.

The following are examples of these three cases:—

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[1] It may not perhaps be superfluous here to point out that the relationships above shortly mentioned are frequently incorrectly stated, because the relationships of position are examined not in the *bud* but in the unfolded leaves. Thus, for example, Wigand (Der Baum, p. 161) was mistaken in saying that the lateral buds of the lime do not begin with the one-half position, having been misled by the torsion of the internodes on the horizontal lateral branches, and having overlooked the fact that the planes of symmetry of the lateral shoot and chief shoot do not coincide from the first. The bud-diagram also which Frank gives (Die natürliche wagerechte Richtung von Pflanzenteilen, Leipzig, 1870, Fig. 1) is not quite right with respect to this point. It is wrong in the position of the axillary buds to the bracts and the position of the first leaves of the bud.

[2] The inflorescences, like those of Vicia Cracca, are all turned to one side, the vegetative buds to the other. Compare Figs. 78, 79.

[3] With reference to this see Reinke, Abhandl. über Flechten IV, in Pringsh. Jahrb. xxviii. p. 191.

(1) Cetraria islandica possesses a dorsiventral flat or upwardly-concave thallus which grows somewhat obliquely upwards. In many of the branches when they grow upwards to a considerable degree the edges of the thallus may become in-rolled and united so as to form a tube, and this is the rule in the variety known as crispa. This kind of thallus-branch always has a radial structure inasmuch as the green algal cells are equally distributed in it, whilst in the dorsiventral branches these algal cells lie chiefly on the upper side. The advantage to the plant from a mechanical point of view of this in-rolling of the edge of the thallus hardly requires mention; it is evident that a thallus-surface can hold itself erect more easily when in-rolled than when spread out.

(2) In Thalloidima vesiculare, club-like outgrowths arise from the thallus which recall many of the lower fruticulose Algae, and in the beard-like lichens the thallus develops from the beginning in this way [1].

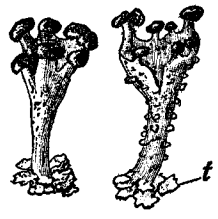

FIG. 31. Cladonia coccifera. A cup-like podetium bearing marginal stalked apothecia rises from the horizontal thallus. (Lehrb.)

(3) In some lichens the stalk of the ascocarp, called the podetium, is strongly developed and of importance as an assimilation-organ, for example in Pycnothelia, Glossodium, and others [2]. If we suppose these podetia to be branched, we should obtain the special form observed in many species of Stereocaulon, where the primary thallus, composed of granules and scales, gives rise to much-branched fruticulose structures, the stronger branches of which bear at the end the fructifications, whilst the weaker portions remain sterile, have limited growth, and serve entirely as organs of assimilation. It is quite the same in the genus Cladonia to which so many species belong [3] (Fig. 31). The starting-point of the development is here also a dorsiventral flat thallus upon which the fructifications sit directly in the simplest cases, whilst in others the fructifications are stalked and branched. Amongst the Cladonieae two chief forms are found which are connected by intermediate states. These are the fruticulose form and the scyphiferous form. In the latter an enlarge-

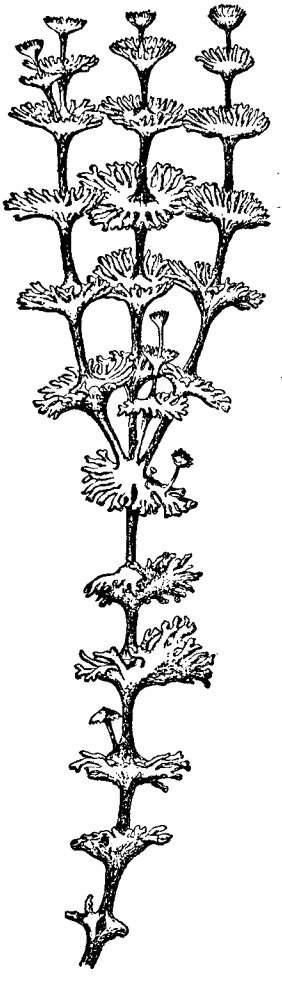

FIG. 32. Cladonia verticillata. Natural size.

[1] See Reinke, Abhandl. über Flechten III, in Pringsh. Jahrb. xxviii. p. 105.

[2] See figures in Reinke, l.c.

[3] See Krabbe, Entwicklungsgeschichte und Morphologie der polymorphen Flechtengattung Cladonia. Leipzig, 1891.

ment of the assimilating surface causes the formation of a cup-like expansion which is a dorsiventral structure, whilst the cylindrical stalk of the cup is radial. This is the case in a special degree in Cladonia verticillata (Fig. 32), in which the stalked cups spring one from the other and give rise to a set of tiers; and, the edges of the cups being slit in a leaf-like manner, the whole habit of the plant is that of one with whorled leaves somewhat like a Chara. This configuration shows us again how from the most different starting-points similar forms may be reached.

In plants without chlorophyll there is nothing comparable with all this as the relationship of surface-growth to light is entirely wanting.

Proceeding now from these general points regarding positions and configurations, the relationships of symmetry of the individual organs will be considered in the following pages under the following headings:—

I. Vegetative organs.
  (*a*) Shoot.
    (1) Radial and bilateral shoots.
    (2) Dorsiventral shoots.
  (*b*) Leaf.
II. Flower and Inflorescence.

II.

POSITION OF ORGANS ON RADIAL AXES.

The arrangement of lateral organs is in but few cases irregular; it usually conforms with definite rules. Thus we see on the roots the lateral rootlets arranged in longitudinal rows in correspondence with the anatomical structure. The arrangement of the leaves on the shoot-axis has attracted special attention. This is not the place in which to set forth the facts which have been obtained in the investigations into the position of leaves, and the explanation which the 'spiral hypothesis' has given to them; enough has been already said upon the subject and there is no necessity for another account here. The spiral hypothesis is however a complex starting-point, and a comprehensive theory of leaf-positions which shall bring all facts into harmony has not yet been framed. As the mechanical hypothesis of Schwendener limits itself to definite cases, and as further research must hinge upon it, an account of it appears to me to be desirable. Dr. Weisse has at my request been so good as to prepare such a statement. I myself hold another view of the importance

of the mechanical hypothesis of phyllotaxy and of its empirical groundwork. I was therefore desirous to have the principles of it explained from the other side.

SKETCH OF THE MECHANICAL HYPOTHESIS OF LEAF-POSITION.

By DR. ARTHUR WEISSE.

The older hypothesis of phyllotaxy occupied itself chiefly with the classification from an arithmetical standpoint of the relative positions of the lateral organs as they were observed in their mature condition. The several arrangements it framed have always a constant value which possess only mathematical relationships one to the other. In sharp contrast therewith is Schwendener's mechanical hypothesis[1] of the position of leaves which is based upon the history of development. In it the lateral organs are not regarded as discrete points but as geometric figures, which at definite stages of development mutually touch, and must therefore influence one another *mechanically*.

Of the factors which cause *displacements* of lateral organs in the course of development of the shoots we must consider as of first importance inequalities of growth in length and in thickness. If we suppose that a mother-organ grows predominantly in thickness, whilst the lateral shoots retaining their form in cross-section increase equally all round, it is evident that the resistances will reach their maximum in the longitudinal direction, their minimum in the transverse direction. The displacements brought about by this will be the same as they would be were the axis subjected to parallel pressure. If, conversely, the growth in length predominates, the displacements that occur will be of a kind such as would be produced by a longitudinal pull.

In order to state the problem as simply as possible we may start, like Schwendener, with the assumption that the form and size of the lateral organs during the displacement remain constant and that their cross-section is circular. Let us consider a concrete case, such as is represented in Fig. 33, which shows a spiral arrangement of the chief series with a divergence of $\frac{13}{34}$, upon a cylindric axis which has been unrolled and spread out. If longitudinal pressure acts upon this arrangement it is evident that it can only be propagated in the direction of those parastichies of which the lateral organs are in contact. We obtain then two components of which the one operates in the direction of the third row (that is to say from organ 27 in the series 27, 24, 21 . . . .), the other in the direction of the fifth row (that is to say from organ 27 in the series 27, 22, 17 . . . .). The problem then is the well-known mechanical one of the movement of a span-roof with unequal length of rafters. In our example organ 27 is the apex, the two contact lines 27, 24, 21 . . . . and 27, 22, 17 . . . . are the rafters of the span-roof. Without following out the mathematical solution of the problem

[1] Schwendener, Mechanische Theorie der Blattstellungen. Leipzig, 1878.

one can easily convince oneself by means of a cardboard model that, in consequence of longitudinal pressure, the angle of the span-roof must increase, and that the foot-points must be pushed away from one another. The apex of the span will then not only sink but will also suffer a lateral displacement in a direction towards the longer rafter. A limit to this displacement is reached in our example when the organ 37 comes into contact with organ 29, and the angle between the third and fifth rows has increased to 120° (see Fig. 34). When this occurs the organs of the third and fifth rows touch not only one another but also those on the eighth row (that is to say 27, 19, 11 . . . .). If the pressure continues the contact with the third row ceases, and the fifth and eighth form a new span in which the features which have been described are repeated. As however the longer rafter will now lie upon the opposite side, the lateral displacement must also take place in the opposite direction. If the apical angle again reaches 120° the thirteenth

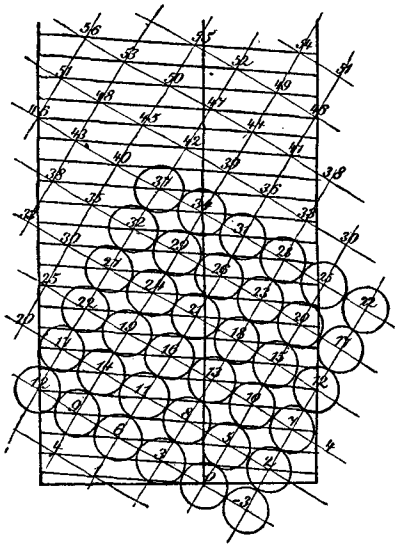

FIG. 33.

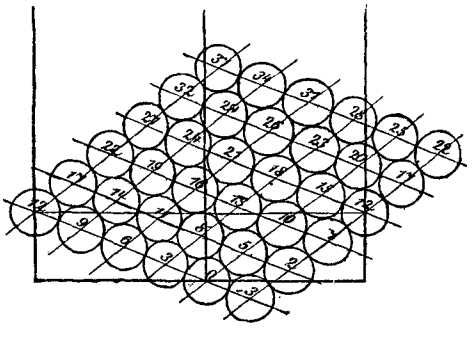

FIG. 34.

FIG. 33. Scheme of the $\frac{13}{34}$ arrangement of cylindric organs. After Schwendener.

FIG. 34. Position of organs derived by longitudinal pressure from that shown in Fig. 33. After Schwendener.

row will come into contact, and if the pressure continues contact with the organs of the fifth row ceases, the eighth and thirteenth row will then form a span, and so on the process will go so long as the longitudinal pressure lasts, and the twenty-first, the thirty-fourth, and the fifty-fifth rows will successively come into contact. In consequence of this alternating combination of the series the single organs move slowly to and fro, oscillating as it were about a middle position. These oscillations however decrease in amount step by step, because the base of the span sinks lower with each change of the contact-line to an always smaller fraction of the original amount. Schwendener has calculated accurately the course of these oscillations. If we start from the $\frac{1}{2}$ position the oscillations always approach more and more the known limiting value of 137° 30′ 28″; the

divergences run successively through all possible values between 180° and this limit. Hence the members of the Schimper-Braun series of divergences

$$\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \frac{13}{34} \ldots$$

have only a special significance in so far as they, being the successive approximate values of the continued fraction

$$\cfrac{1}{2+\cfrac{1}{1+\cfrac{1}{1+\ldots}}}$$

through which as is well known the above-mentioned limiting value can be exhibited, express *approximately* by the smallest figures the actual divergences.

What has been shown in this example for the positions in the chief series holds in general also for every other spiral system. A longitudinal pressure produces always a gradual approximation to a certain limiting value, and that a longitudinal *pull* must bring about displacements in reverse succession goes without saying.

We have hitherto assumed for simplicity's sake that the lateral organs are constant in diameter and that the circumference of the mother-organ only is variable. But such a supposition represents no real case; the shoots grow always so strongly that the mutual distances in the longitudinal direction become also gradually greater. Whilst then the angle of the given span in consequence of the predominating growth in thickness of the stem opens more and more, the two rafters lengthen at the same time. Instead of a sinking of the apex as has been above depicted there is, as a matter of fact, a gradual rising of the gable. The *lateral* oscillations however will attain in this case also the same amount, as they depend only upon the mutual relationships of the length of the rafters.

The circular cross-section hitherto supposed for the lateral organs is almost completely realized in many cases in nature, especially in the region of the flower, but in numerous other instances in which the organs appear to be more drawn out in breadth or in length we cannot assert this without further inquiry. If the organs have an elliptic transverse section the following considerations will lead us to a solution of the problem. We can imagine an elliptic system arising if we project upon an oblique plane the scheme that we construct for organs with circular cross-section. If we consider, for example, the shadows of a circular system which are projected by the sun's rays we can easily satisfy ourselves that upon inclined projection-planes the circles pass over into ellipses of similar excentricity. The angle formed by the rafters suffers in this way important changes; in transversely-placed ellipses the height of apex is diminished, in erect ellipses it is increased; the lateral oscillations however remain the same in both cases as they are in circular organs. The same is true for other closed figures of regular form so long as the transverse axes are placed horizontally. The lateral displacements in the case of axes lying obliquely exhibit on the other hand small deviations. Still in this case also the chief character of the oscillations remains

the same. In nature, however, markedly obliquely-placed organs occur relatively seldom.

Few organs retain during the whole course of their development the same form. Most of them show considerable changes which are partly active, brought about by growth, partly passive, flattenings caused by reciprocal pressure. In many cases these attain to such a pitch that the circular transverse sections of the primordia become polygonal at an early period, and they lie touching one another without interspaces. The cones of many Coniferae, the heads of Compositae, the fruit of the pine-apple, furnish examples. In these cases there is contact of the organs in three directions usually during a long period, and we have then in a certain degree to deal with a span-roof with three rafters. As Schwendener has shown, the lateral displacements suffer then generally a diminution; the approximation to the limiting value takes place with oscillations of small width.

Having in what precedes dealt with the displacements which a given arrangement of lateral organs experiences in course of the development, let us now turn our attention to the *mode of installation* of the primary positions. Observations of the apex of shoots teach us that new organs are always laid down upon them in connexion with those which precede them in acropetal serial succession. Hofmeister[1] was the first who endeavoured to give a mechanical explanation of this fact in his dictum that new organs arise in the widest intervals that occur between the organs already existing. Whilst this statement cannot be accepted now in the form in which it was made, yet we must acknowledge that Hofmeister rightly recognized that the position of new organs is conditioned by that of the older ones. Schwendener has carefully investigated these relationships in many examples, and he has shown it to be a general rule that *the young organs are laid down in contact with the older.* In order to avoid misunderstanding it is necessary to state specifically that this contact of the young papillae of the leaves generally takes place only in two parastichies, and that there is no contact as a rule of the orthostichies. Of course one cannot speak of a literal contact of the primordia until they appear upon the surface of the mother-organ, yet as a matter of fact the youngest stages of lateral organs can be recognized through the microscope at a much earlier period; their centres of formation can be seen at certain distances from one another so that every primordium occupies a definite developmental field which it completely fills up in the course of its construction but cannot overstep because the adjacent primordia claim completely the areas that in like manner belong to them[2]. That these areas of development have a definite size, and so long as the organs are similar an almost constant size, is a morphological fact requiring no further explanation, no more than does that of the mutual limitation of these areas and the contact of the juvenile organs which results from this. *The relative size* of the primordia and their *contact* with preceding organs

[1] Hofmeister, Allgemeine Morphologie der Gewächse. Handbuch der physiologischen Botanik, i. Abt. 2. Leipzig, 1868.

[2] Schwendener, Die jüngsten Entwickelungsstadien seitlicher Organe und ihr Anschluss an bereits vorhandene, in Sitzungsber. d. Berliner Akademie d. Wissensch., 1895, p. 645.

are the morphological ground-work upon which Schwendener has built up his limitation-theory.

It has been already stated that this contact is observed in the parastichies but not as a rule in the orthostichies; the three-ribbed species of Cacteae amongst the Spermaphyta are however an exception to this[1]. In them the three orthostichies are contact-lines whilst a lateral contact cannot be established even in the very youngest primordia of the leaves. The formation of the ribs must in this case have a definite influence upon the procedure at the apex, although they only begin beneath the uppermost leaf-primordia. The absence of lateral contact has only been certainly established for the three-ribbed forms; in the four-ribbed, and still more in the five-ribbed, shoots of Cacteae the young primordia touch each other in the lateral direction. Variations in the number of the ribs are found not infrequently as is well known in the same shoot; a four-ribbed portion, for example, may suddenly appear between three-ribbed ones, or a rib may cease with a definite leaf-cushion. Changes of the leaf-position are of course associated with such transitions, but the changes are not in these cases brought about by mechanical causes—they are relations of a morphological kind. From Vöchting's interesting investigations[2] we learn that the form of the shoots of the Cacteae is in a very striking manner dependent upon the intensity of the illumination.

Whilst in Spermaphyta, apart from the exceptions mentioned above, every point of the apex has a like capacity to become the centre of a new group of formations, we find in certain cryptogamous plants a definite relationship between the position of the lateral shoots and the process of segmentation which takes place at the apex. In the mosses, for example, it is well known that a leaf proceeds from each segment that is cut off from the apical cell, but in the Pteridophyta on the other hand a dependence upon cell-division of the apex is no longer visible. It is easy to convince oneself that the spiral in which the segments in the apical cell of the stem of a fern follow one another is by no means always directed in the same way as the leaf-spiral; homodromy and heterodromy are about equally common. Struthiopteris germanica furnishes an instructive example, for in it the apical cell is *two-sided* whilst the leaves have a *spiral* arrangement with the divergence of the chief series[3].

We have previously seen what displacements organs are subjected to in the course of their development when the relationship of their size to the circumference of the mother-organ is changed by its unequal growth in length and thickness, and quite analogous changes of position must result if the relative size of the lateral organs be changed from any other cause. If, for example, the lateral organs gradually become smaller at a definite period of the development, say, at the

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[1] Schwendener, Zur Kenntnis der Blattstellungen in gewundenen Zeilen, in Sitzungsber. d. Berliner Akademie d. Wissensch., 1894, p. 974.

[2] Herm. Vöchting, Über die Bedeutung des Lichtes für die Gestaltung blattförmiger Kakteen. Zur Theorie der Blattstellungen, in Pringsh. Jahrb. xxvi (1894), p. 438.

[3] Schwendener, Über Scheitelwachstum und Blattstellung, in Sitzungsber. d. Berliner Akademie d. Wissensch., 1885, p. 927.

point where the transition takes place from the region of the foliage-leaves to the region of the flower, or if these organs remain equally large whilst the common axis increases in circumference, changes of position will take place which conform in all essentials with the displacement brought about by longitudinal pressure; the only difference being that the changes which in the latter case must affect the *same* organs *one after the other* are here observed in *different* organs *beside* one another.

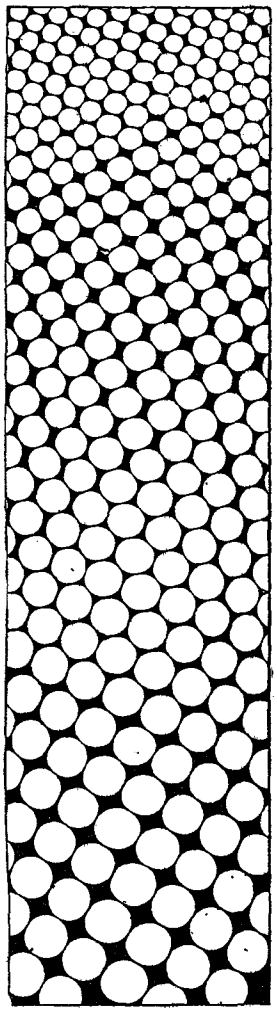

FIG. 35. Scheme to exhibit the consequence of the gradual decrease in size of cylindric organs. After Schwendener.

Fig. 35 gives a representation of the effect of gradual decrease in size of organs having a circular outline in cross-section. In the lower part of the figure, at *A* the third and fifth rows are in contact and cut one another at about a right angle; at *B* the fifth and eighth parastichies do this; whilst at *C* the eighth and thirteenth touch one another but cut at an oblique angle. Between these we find at α and β positions of transition in which the organs are in contact in three directions. The rows thus come to occupy quite the same position and therefore to have the same divergences as we have already noticed in the displacement of organs of equal size in consequence of predominant growth in thickness of a mother-organ.

If the organs become small very rapidly, groupings may arise which require special consideration. According to the degree of diminution links are obtained which Schwendener has designated first, second, and third *transition-figures*. Cases of the third kind are very rare in the plant-kingdom and we shall confine ourselves therefore to an account of the first and second only. Fig. 36 gives a representation of the *first transition-figure*. In the space bounded by the lower three ellipses an organ appears which touches two of the ellipses, whilst a third organ stands in contact with it and the third ellipse. According to the numbering of the ellipses which has been chosen in the figure the contact ceases in the fifth row, and is renewed in the thirteenth row. In the case of the *second transition-figure* represented in Fig. 37, two organs appear in the space but do not completely fill it up, so that a third organ can appear between these but it does not touch the lowermost ellipse. The numbers of the ellipses in this figure show that the contact ceases here both in the fifth and in the eighth row but is renewed in the thirteenth and twenty-first. In the advance of the contact-lines here an entire step of the intermediate positions is skipped over. It fits in to a certain extent with the position at *A* in Fig. 35,

as well as with that at *C*. It is worthy of remark that the changes of position associated with so rapid a decrease in size of the organs proceed in the path of the recurrent series we have considered. The heads of Compositae especially supply examples of this in the region where the first flowers are in contact with the

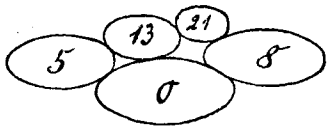

FIG. 36. First transition-figure. After Schwendener.

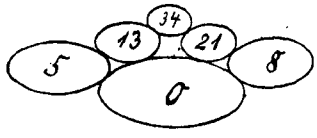

FIG. 37. Second transition-figure. After Schwendener.

enveloping bracts; so also do the bases of cones of Coniferae at the point of connexion of the scales of the cone with the bracts of the stalk.

We have concerned ourselves hitherto only with spiral positions, a few words are now necessary regarding *cyclic* positions.

If we leave aside the relatively rare twisted whorls (the bijugate and trijugate systems of the brothers Bravais), as well as some irregular arrangements within flowers, we may lay down the rule that members of the several whorls alternate with one another, that is to say, the organs of one whorl stand over the gaps between the members of the preceding whorls. The contact-lines run in this case to both sides with the same angle; they form then a span-roof with rafters of equal length which can give no occasion to lateral displacements. A change of the position must on the other hand ensue so soon as the relative size of the organs changes in the direction of a parastichy. Displacements of this kind are often seen in the spadices of Aroideae. Fig. 38 is a diagram of such a case. The lower part shows five-membered whorls, the upper shows a spiral arrangement with a $\frac{2}{9}$ divergence. The number of the organs in a complete cycle is here less than double the number of members in a preceding whorl. In an analogous manner by a corresponding increase of the relative size of the organs in a four-membered whorl, there may result a $\frac{2}{7}$ spiral; and generally upon whorls with n members there follows a spiral arrangement with the divergence $\frac{2}{2n-1}$. If

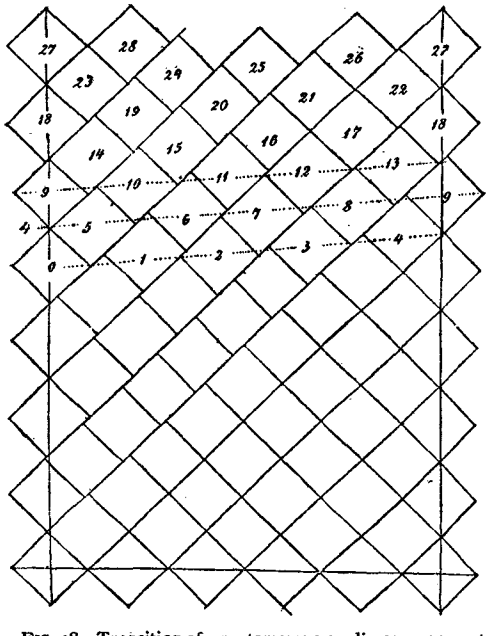

FIG. 38. Transition of a pentamerous cyclic arrangement into a spiral one with a divergence of $\frac{2}{9}$. Diagram based upon observations on the spadix of Aroideae. After Schwendener.

on the other hand the relative size of the organs decreases in the way supposed, a four-membered whorl will give a spiral arrangement with the divergence $\frac{2}{5}$, a five-membered one will result in a spiral with a divergence of $\frac{2}{11}$, and generally upon whorls with n members a spiral with the divergence $\frac{2}{2n+1}$ will follow. In the Aroideae the changes in size are commonly found, but irregularly, so that, as there are many transitions, spirals of other series appear.

The Aroideae may serve also to illustrate a further cause of change of position, namely, the *abrupt diminution in size* of organs. The amplexicaul spathe is followed, as is well known, without interruption by the relatively small flowers. The spathe being commonly obliquely inserted, the first flowers which shoot out close above its base are unable to form a complete whorl or the whole cycle of a spiral, consequently the regular positions are observed only at some height above the base. The great variety of systems which is found in the spadices of the Aroideae is easily understood through the mechanical hypothesis of leaf-position. The small individual deviations in respect of the insertion of the spathe and the size of the primordia of the flowers must necessarily lead to the most different relationships of position.

Let us now turn to the peculiarities exhibited by the position of leaves in relation to the *branching of the stem.*

In the rare cases of *dichotomous* branching, as they are seen in Lycopodieae, the primordia of the leaves on the branch after forking are linked on without interruption to those of the undivided branch. If the angle of the successive dichotomies is somewhat acute so that the branches at first touch one another, there can be no leaf-formation at this place, and in consequence gaps arise here, which may give occasion to a variety of changes of the arrangement which was previously followed. The connexion however always conforms with the rules of the juxtaposition.

With regard to the more common case of *axillary* branching, it is evident that the apex of a bud wedged in between a mother-shoot and an axillant leaf experiences less pressure in the lateral direction than in the median; the first two leaves of the axillary shoot are therefore most usually *lateral*, and only the succeeding leaves are *median*, or more or less oblique. If the phyllotaxy is spiral the third leaf has an alternative position. It may shoot out upon that side of the axillary bud which is next the stem, or upon that which is next the axillant leaf, and then there may be displacement towards the right or towards the left of the median. The inequality of pressure to which the bud is in general subjected upon its anterior and posterior sides is partly a consequence of the dissimilarity of the organs which exercise the pressure, partly of the direction of growth of the bud itself, and this is determined by its morphological nature. According to circumstances then that amount of diminution of pressure which is a condition in the formation of lateral shoots takes place in one plant first of all upon the anterior side, that is between the bud and the axillant leaf, whilst in another plant it takes place first of all on the posterior side, that is between the bud and the mother-axis; and it is possible that in the same plant sometimes the one side, sometimes the other is the more favoured. As we cannot of course measure

accurately the degree of pressure to which the bud is subjected on the anterior and on the posterior side, we must seek for aid in this matter from indirect evidence, and especially from that afforded by extreme cases in which the different relationships of pressure can with some certainty be observed. If the lateral shoot in its growth forms almost a right angle with the chief axis, there occurs at a very early period cessation of contact between the mother-axis and the apex of the axillary bud, whilst the contact with the axillant leaf persists for a longer time. In such a case the third leaf will of necessity appear upon the posterior side, and it is found in this position without exception in all plants which possess these conditions. Schwendener has described a large number of cases, especially in the Coniferae and Crassulaceae. In other plants whose axillary shoots are less vertical, this disposition is less constant, as is to be expected. If the axillary bud shoots out from the mother-axis at a relatively acute angle, the third leaf is always on the side next the axillant leaf, and this position is characteristic of the majority of dicotyledonous plants. The *lateral deviation* of the third leaf is brought about by the *asymmetric relationships* of the leaf-axil, and three of these are of chief importance:—

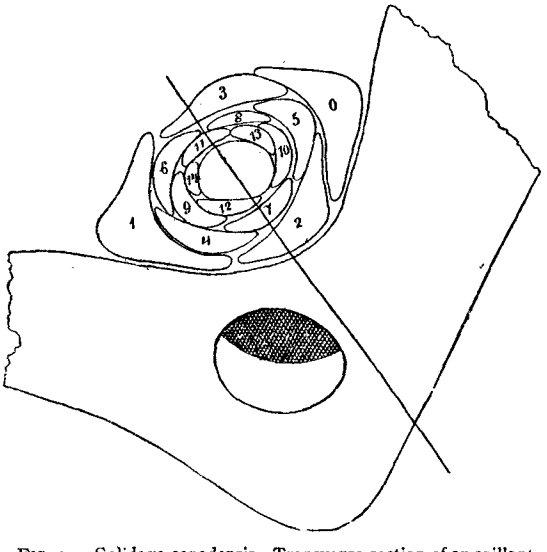

FIG. 39. Solidago canadensis. Transverse section of an axillant leaf and its axillary bud. Magnified 45. After Schwendener.

1. A lateral displacement of the median of the axillant leaf with respect to that of the mother-stem and the axillary bud.

2. An oblique insertion of the axillant leaf.

3. The spiral position of the bases of the leaves of the mother-axis above the axillant leaf through which unequal pressure is exercised upon the axillary bud.

The first two kinds of asymmetry are common, the third has only been observed so far in the inflorescences of Coniferae. Fig. 39, which is a cross-section through the axillary bud of Solidago canadensis along with its axillant leaf, will enable us to follow the effect of such asymmetric relationships. The median of the axillant leaf lies evidently to the left of that of the stem and bud, which is indicated in the figure by the straight line. Upon this side the axillant leaf will evidently exercise a greater pressure upon the bud than it does upon the right side, and therefore the third leaf, indicated by 2 in the figure, must arise upon the right side. The following leaf, which is towards the posterior side, appears to be displaced to the same side of the median, and the position of the third leaf determines the direction of the spiral: it is in the case before us dextrorse. I must refer for further details to the original works[1].

[1] Schwendener, Mechanische Theorie der Blattstellungen, p. 98; A. Weisse, Beiträge zur mecha-

The installation of and the direction of the leaf-spiral are also affected by asymmetric relationships on the *axis of the seedling*[1]. In dicotyledonous plants the two cotyledons often show slight deviations from regular opposition and the effect of this is visible in the arrangement of the very first foliage-leaves; but in other cases the first leaves are more or less regularly decussate, and the decussation only gradually suffers disturbance through the slight irregularities which are always to be observed in organized structures, and is followed usually by a number of leaves irregularly placed until finally a definite spiral position is attained.

The position of the first leaves in *adventitious twigs* is also dependent upon mechanical relationships. Some experimental investigations which I have made with cuttings of willow are so interesting in this respect as to be worthy of note here[2]. If all the axillary shoots be removed from a cutting after it has rooted, adventitious shoots soon form, chiefly on the cut surfaces. By varying the form of the wounded surface, one can frequently cause variation in the base of the adventitious shoot and thus experimentally modify its influence upon the position of the first leaves. The first leaf is always laid down at the place of least resistance; but with regard to the position of the following leaves further experiment is wanted before a definite conclusion can be come to; they often stand irregularly and it is only gradually, as on the axis of a seedling, that they fall into a definite arrangement.

The frequent appearance, amidst such changing transitions, of organs in positions referable to the chief series, is partly dependent upon the relative size of the organs, partly upon the basis upon which the system is built[3]. It would however carry me too far to go into this question.

The relationship of form and of size of the base of the young leaf is the most important element in bringing about in one species regular spiral position of the leaves, whilst in another the distichous or the cyclic arrangement prevails[4]. If the primordia of the leaves grow at an early period predominantly in breadth, that is, in a direction transversely tangential to the apex of the stem, so that they embrace more than a half of it before the following leaf shoots out, there arises, if there be symmetric construction of the sides of the leaf, a *distichous* arrangement. On the other hand, if the growth of the young primordia is predominant in thickness, that is to say, in a direction radial to the apex of the stem, then generally *leaf-pairs* and *whorls* arise. The number of members of any one whorl is dependent upon

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nischen Theorie der Blattstellungen an Axillarknospen, in Flora, 1889, p. 114; Id. Über die Wendung der Blattspirale und die sie bedingenden Druckverhältnisse an den Axillarknospen der Coniferen, in Flora, 1891, p. 58.

[1] Schwendener, Wechsel der Blattstellungen an Keimpflanzen von Pinus, in Sitzungsber. d. bot. Vereins d. Provinz Brandenburg, xxi (1879), p. 109; Bernh. Rosenplenter, Über das Zustandekommen spiraliger Blattstellungen bei dikotylen Keimpflanzen. Inaug.-Dissertation. Berlin, 1890.

[2] A. Weisse, Neue Beiträge zur mechanischen Blattstellungslehre, in Pringsh. Jahrbücher, xxvi (1894), p. 238.

[3] Schwendener, Zur Theorie der Blattstellungen, in Sitzungsber. der Berliner Akad. d. Wissensch., 1883, p. 750; A. Weisse, Neue Beiträge zur mechanischen Blattstellungslehre, in Pringsh. Jahrb. xxvi (1894), p. 256.

[4] A. Weisse, Neue Beiträge zur mechanischen Blattstellungslehre, in Pringsh. Jahrb. xxvi (1894), p. 236.

the relative size of their primordia as well as upon the mechanical relationships of their bases. Thus, in a decussation of leaf-pairs the axillary shoots should have relatively large primordia of leaves and submit to nearly equal pressure from the mother-axis and from the bract. The *spiral positions* finally, are, as has been so frequently stated, always accompanied by asymmetry which exists either at the base of the axis under consideration or appears in its further development. The growth in thickness and in breadth of the young leaf-base appears to be in these cases of medium amount.

The beautiful results which the mechanical hypothesis of the position of leaves has furnished in the domain of the morphology of the flower[1] must be passed over here, because they have to do less with principles than with interesting details with which it is impossible to deal shortly.

III.

DORSIVENTRAL SHOOTS.

The difference between the dorsal and ventral sides of dorsiventral shoots may be expressed in (1) the *structure* on the two sides, or in (2) the *position of their members.*

1. Different Structure of the Upper and Under Side.

The different structure of the two sides of a dorsiventral body is well seen in the thallus of a liverwort, or in a shoot with distichous leaves where the upper surfaces of the whole of the leaves are turned upwards and the under surfaces are turned downwards. In less striking degree the dorsiventrality appears in the *shoot-axes of leafy shoots;* but it is quite evident and shows itself partly in the configuration, partly in anatomical structure. The axes of the leaf-like shoots of Phyllanthus lathyroides are flattened on the upper side like many leaf-stalks; their structure is not unlike that of the axes of many dorsiventral inflorescences[2]. The dorsiventral axes of Hypnum splendens are flattened upon the upper side in like manner. With regard to the behaviour of the Lycopodieae see page 102. In the orthotropous shoots of trees the wood is usually radially developed; plagiotropous lateral branches very often show the phenomena which C. Schimper described[3] as epinasty and hyponasty,

[1] Schwendener, Mechanische Theorie der Blattstellungen, p. 107; K. Schumann, Blütenmorphologische Studien, in Pringsh. Jahrb. xx (1889), p. 349; Id., Neue Untersuchungen über den Blütenanschluss, Leipzig 1890; Id., Morphologische Studien, Heft 1, Leipzig, 1892; A. Weisse, Die Zahl der Randblüten an Kompositenköpfchen in ihrer Beziehung zur Blattstellung und Ernährung, in Pringsh. Jahrb. xxx (1897), p. 453.

[2] See Goebel, Über die Verzweigung dorsiventraler Sprosse, in Arb. d. bot. Instituts in Würzburg, ii. p. 430.

[3] C. Schimper, Amtlicher Bericht der Naturforsch.-Versammlung in Göttingen, 1854; Hofmeister,

that is to say, the wood grows more towards the upper or towards the under side and thus the pith acquires an excentric position. I may mention here, quoting Wiesner, the following facts regarding the plagiotropous shoots of trees and shrubs:—

(1) The Coniferae are hyponastic.

(2) Broad-leaved trees with feebly developed or no anisophylly show at first a radial condition of the wood, whilst later it is epinastic and finally is hyponastic.

(3) Broad-leaved trees with strong anisophylly are at first hyponastic, then become epinastic, and finally hyponastic again.

(4) In many shrubs, for example Lycium barbarum and Berberis vulgaris, the axes remain radial.

We do not know the causes which bring about the epinasty and hyponasty; it is only clear that plagiotropous growth excites it. The phenomena of varying predominance in growth of the upper and the under side are exhibited not only by the wood but appear also elsewhere. We see them in the secondary rind in many woody plants and in the peripheral fundamental tissue upon the upper and the under side of young shoots. The creeping shoots of Nuphar luteum have a radial terminal bud, but they subsequently become dorsiventral and creep upon the soil under the influence of unilateral illumination, as will be shown in the Fifth Section; the leaf-scars upon the upper side are then far apart but are more closely set on the under side. The needles in many Coniferae (spruce, yew, and others) show like features, only not so strongly, and they are also to be found on the plagiotropous shoots of Elatostemma and Goldfussia anisophylla.

2. Relationships of Position.

The dorsiventral construction expresses itself, in the second place, in the different relationships of position of the lateral shoots of the two sides. By 'dorsal side' in creeping, climbing, and swimming shoots we mean the upper side, the ventral side is the under side. A peculiarity of the vegetative point which we meet with in a number of dorsiventral shoots belonging to the most different divisions of the Vegetable Kingdom is often associated with the difference in these two sides, namely, a strong incurving or involution of it which secures the protection of the embryonal tissue. A similar feature is observable in the leaves of ferns, species of Drosera, and other plants. In Fig. 40 there is a representation of such

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Allgemeine Morphologie, p. 604; Kny, Über das Dickenwachstum des Holzkörpers, in Sitzungsber. d. Gesellsch. naturforsch. Freunde zu Berlin, 1877; Wiesner, Untersuchungen über den Einfluss der Lage auf die Gestalt der Pflanzenorgane, in Sitzungsber. der Wiener Akad. 1892. Wiesner has introduced the terms 'epitrophy' and 'hypotrophy' for epinasty and hyponasty, as the latter have been applied in a different sense.

an involution of the vegetative point in the alga Cliftonaea pectinata, and Polyzonia jungermannioides shows the involution to an even greater degree; amongst the Bryophyta, examples are found in Mastigobryum and Hypnum crista-castrensis; amongst the Pteridophyta, in Azolla; amongst the Spermaphyta, in the aquatic species of Utricularia.

The dorsiventrality of vegetative shoots, and especially the position of their organs, can usually be brought into evident relationship with the conditions of life, and the examples we are about to quote will show this without further explanation. Such a relationship is not however always visible, probably on account of our incomplete knowledge of the conditions of life in the plants concerned, although it is at the same time possible to conceive that dorsiventral configuration depends upon 'inner' causes

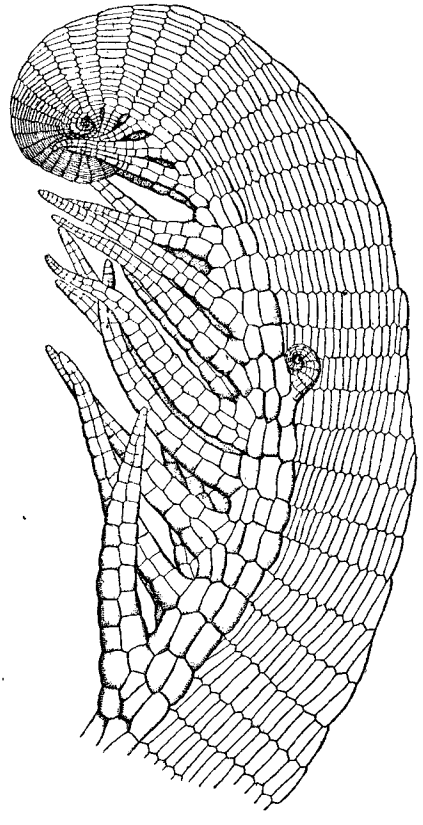

FIG. 40. Cliftonaea pectinata. Apex of one of the dorsiventral shoots.

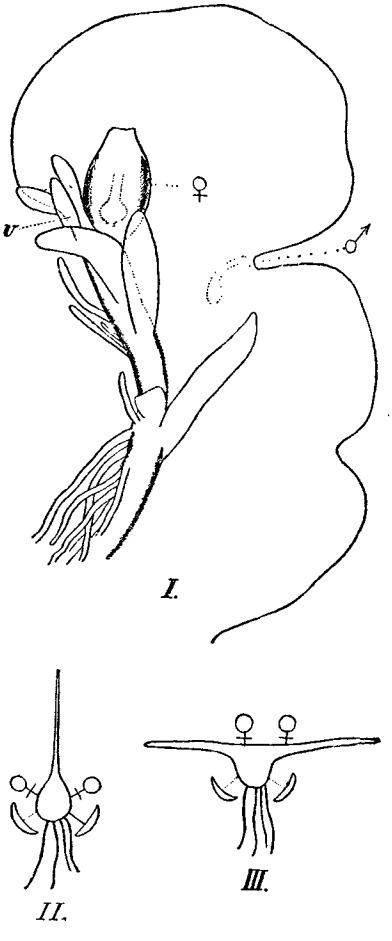

FIG. 41. *I* Riella Battandieri. Upper part of a plantlet. At ♂ the position of an emptied antheridium. At ♀ a young sporogonium. *v* vegetative point. Magnified. *II* Scheme of Riella. *III* Scheme of another thallose liverwort; the thallus seen in transverse section.

without direct relationship to the outer world. Some marine Algae in which we frequently can see but little relation to the environment may be examples of this. Thus Rytiphloea pinastroides[1] possesses non-creeping shoots which are free in the water and have dorsiventral involute terminations like croziers. The lateral shoots stand upon the flanks towards the concave side; short shoots ('leaves') of simple construction stand upon the convex side. The former, along with the involution, protect the vegetative point, but I must leave as an open question whether this is the only biological significance of the dorsiventrality. Cliftonaea pectinata, the alga represented in Fig. 40, has one side developed as a wing which is evidently vertical in profile.

A remarkable parallel formation is seen in the liverwort Riella (Fig. 41). The shoots here are also dorsiventral, but the dorsal side is not flat as is the case in other dorsiventral liverworts, it is developed as a wing when seen in profile[2]. We find similar arrangements in leaves, for example the leaf-surface in Fissidens and Iris corresponds with the wing in Cliftonaea and Riella.

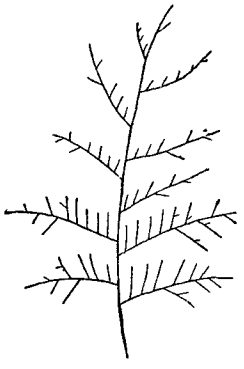

FIG. 42. Thuya occidentalis. Scheme of the position of the twigs on a lateral shoot. The first branches of the third order stand on that side of the branches of the second order which is turned towards the chief axis.

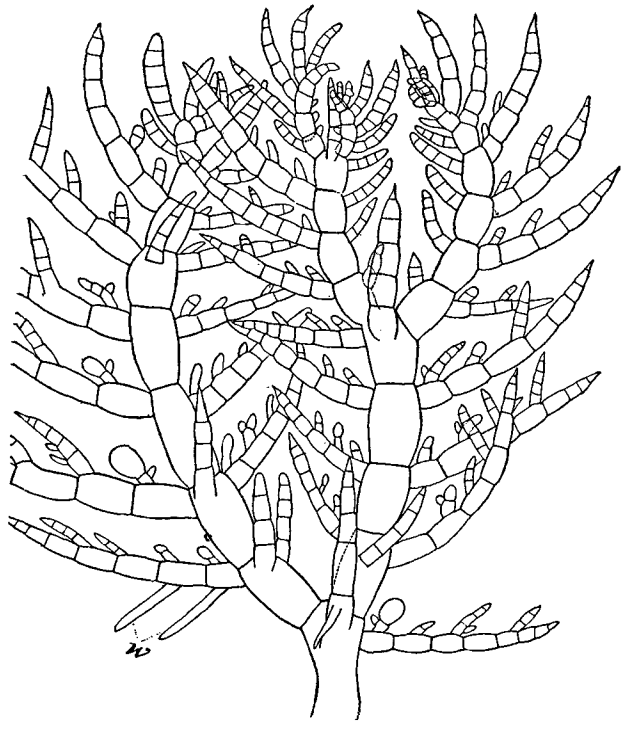

FIG. 43. Antithamnion (Pterothamnion) Plumula. Portion of the thallus. The small cells with peculiar contents are not shown. Highly magnified. The explanation of the figure will be found in the text.

[1] See for this and some other analogous cases—Ambronn, Über einige Fälle von Bilateralität bei den Florideen, in Botan. Zeitung, 1880, p. 160.

[2] For the details see Part II of this book.

In lateral shoots, and in lateral members generally, there is a dorsiventral construction which stands in a definite relationship to the chief shoot, although as yet it is impossible to declare that this relationship is anything else than a mere superficial one—one depending upon the conditions of space available. Fig. 42 is a diagram taken from an individual instance of the branching of a shoot of Thuya occidentalis. Each lateral shoot is at first dorsiventral and its first three to five branchings appear only on the side turned towards the mother-shoot,

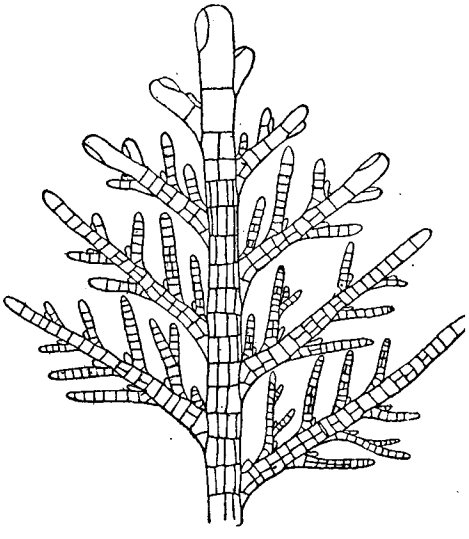

FIG. 44.

FIG. 44. Halopteris filicina. Apex of a long shoot. Magnified.

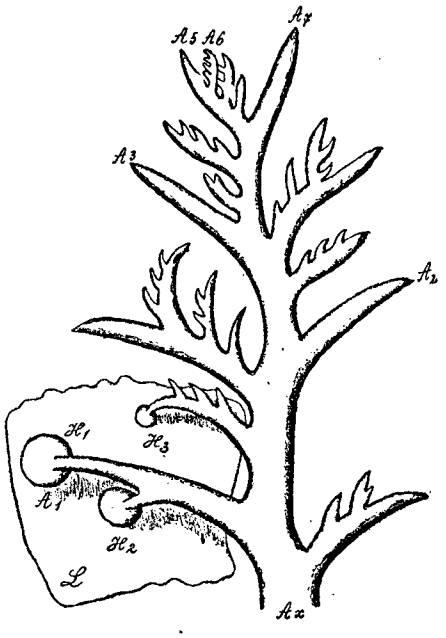

FIG. 45.

FIG. 45. Plocamium coccineum. The lateral branches always stand upon one side, the growth is sympodial. At H_1, H_2, H_3, are anchoring discs by means of which the plant is attached to another alga (L). Magnified.

the later ones stand alternately on the two angles, and we cannot suppose that this unilateral position at the beginning of the shoot is the result of an influence either of gravity or of light. The same thing is found in many Algae. Compare, for example, Fig. 44, representing Halopteris filicina [1], which has the lowermost lateral branches of each primary branch turned towards the chief axis, the following ones alternating; the same is found in Euptilota (shown in Fig. 46) where the outer side has preference.

[1] Out of 44 examples of Stypocaulon examined by Geyler the first branch of the second order upon branches of the first order was directed outwards in 8, directed inwards in 36. There was here then overwhelming preference for the inner side, but no constancy. See Geyler, Zur Kenntniss der Sphacelarieen, in Pringsh. Jahrb. iv. See also Berthold, Beitr. zur Morphologie und Physiologie der Meeresalgen, in Pringsh. Jahrb. xiii.

We find it also in many leaves. Whilst we may hold that this position is utilitarian because the development of the branches on both sides would bring about an overlapping of them which would interfere with their function, we cannot yet say anything about the original conditions under which it arose. The case of Antithamnion Plumula, represented in Fig. 43, is specially striking. Long shoots and short shoots[1] are seen here; some short shoots stand on that side which is in the plane of the paper, and these form the special framework of the plant, others occur upon the other surfaces both above and below. The latter are in much smaller number and serve as it appears only as a protection to the young parts, as they are specially found in the positions where a lateral long shoot is formed. In the long shoots the branching is predominant upon the outer side and is retarded upon the inner side, whilst each short shoot produces branches only upon the side which is turned to the chief axis. Euptilota Harveyi, represented in Fig. 46, shows a predominance of the branching on the outer side of the long shoot[2].

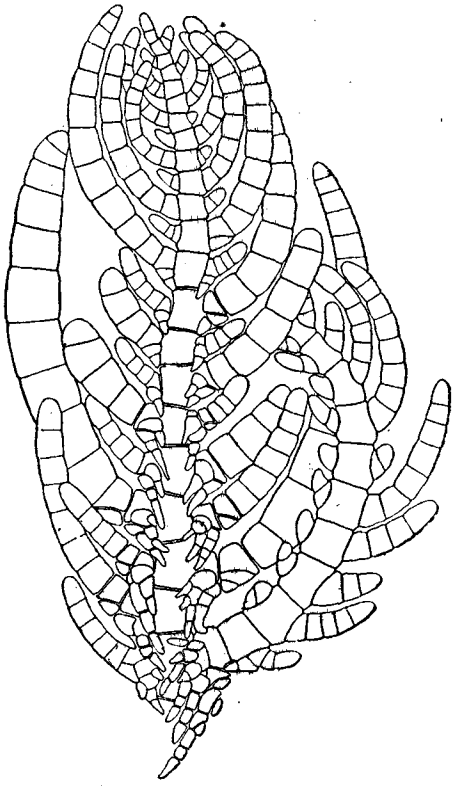

FIG. 46. Euptilota Harveyi. Apex of a long shoot. On each segment there are two unequally sized short shoots. Below on the right a long shoot has developed, the lateral branches of which are arrested upon the side of it turned towards the chief axis. After Cramer.

Whilst now the immediately inciting causes of these phenomena are unknown, and we can only say of them as of the segmentation of many leaves that they result in one of the many possible constructions by which the best use of the space available is secured, it may not be superfluous to remark that relationships lie before us here which repeat themselves in the same way in the lower and in the higher plants, and that they offer therefore a subject for the most searching examination.

In the following pages the more important forms of dorsiventral construction will be dealt with. It is scarcely possible to group them

[1] See page 35.

[2] See the right lower side of Fig. 46.

in sharply defined categories, and the following arrangement is merely a convenient one:—

A. Creeping and climbing shoots.
B. Dorsiventral lateral shoots.
C. Anisophylly.

Anisophylly is found both in creeping and climbing chief shoots and in dorsiventral lateral shoots, and I only treat of it here as a special category because of its common occurrence. Asymmetric leaves are another peculiarity of many dorsiventral shoots, and they will be spoken of in the chapter on the relationships of symmetry of leaves (see p. 114).

A. CREEPING AND CLIMBING SHOOTS.

The dorsiventrality of these shoots shows itself in the presence of the roots upon the ventral side, turned away from the light, in the manner in which we find them in the thallus of a liverwort, on the prothallus of a fern, and also in many higher plants. The relationship of this construction to light will be discussed in the Fifth Section. A second indication of the dorsiventrality of these shoots is the 'tendency' to displacement of the leaves towards the upper side, whilst the lateral shoots remain upon the flanks, and there is a remarkable agreement in the occurrence of this in the most different cycles of affinity of plants. We can, as so often happens, distinguish two cases here—either this position of the organs is acquired in course of their individual development, or it is fixed from the beginning at the vegetative point.

Two examples of bilateral shoots with distichous phyllotaxy may be cited in illustration of the first case. Monstera deliciosa, one of the Aroideae, possesses climbing shoots the leaves of which are so displaced to the dorsal side, chiefly through torsion of the internodes, that they often appear as if they were in one row. We find the same in the creeping shoots of Acorus and Butomus. In Butomus umbellatus the creeping shoot has an erect terminal bud in which the leaves are in two rows and the primordia of the lateral shoots stand in the median plane of the leaves; but on the prostrate portion of the rhizome the leaves stand in two rows closely approximated upon the dorsal side, and the lateral buds are found upon the flanks at the lower edges of the leaves, while the ventral side appears to be quite free from leaf-insertions and bears only roots.

In the second case the position of the organs is quite similar. Caulerpa prolifera, one of the Siphonieae, possesses a creeping stem which bears upon its ventral side 'roots,' on its flanks twigs, and on its dorsal side 'leaves' (Fig. 47). The floridean alga Herposiphonia shows the same thing, having two rows of 'leaves' upon its dorsal side, lateral

shoots upon the flanks, and 'roots' upon the ventral side. The relationships of position which occur in the creeping stems of Marsilia and Pilularia, among the Filicineae, are similar. Other creeping stems of ferns, like those of Lygodium palmatum, Polypodium Heracleum, and Polypodium quercifolium[1], have the dorsally-placed rows of leaves so near one another that they appear as if there was only one row, whilst in Polypodium taeniosum the parastichies of leaves stand close together on the dorsal side only. The germ-plants of Polypodium Heracleum, which were investigated by Klein, have a distichous phyllotaxy with a divergence of the rows of about 45° upon the dorsal side, so that the dorsiventrality is less sharply marked in them than in the older plants which have a monostichous or nearly monostichous phyllotaxy. In all these ferns the dorsiventrality is already fixed at the vegetative point and is not the result of subsequent displacement. The lateral shoots of these ferns are placed nearly on the flanks. Analogous relationships of position are also found among flowering plants, in species of Begonia, for example, with thick fleshy creeping stems; the Podostemaceae also, which cling to their substratum, often show dorsiventral construction[2], and other examples will be occasionally mentioned in the course of this account[3].

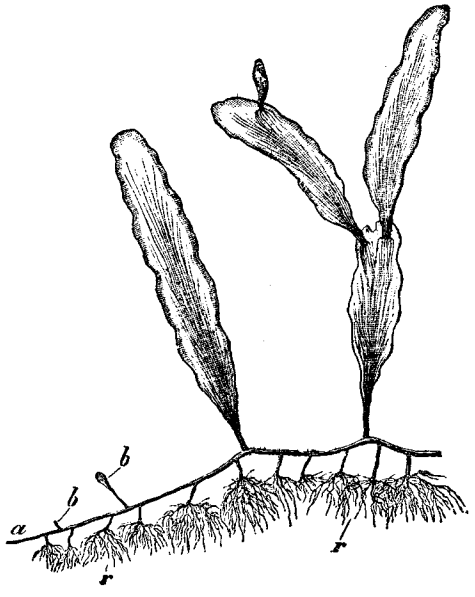

FIG. 47. Caulerpa prolifera. Habit. The creeping shoot-axis (*a*) bears leaves (*b*) above and roots (*r*) below. Lehrb.

The facts which have been mentioned should suffice to show how widely spread dorsiventral construction is in creeping and climbing plants in the most different cycles of affinity; and it is clearly the most advantageous one, for the leaves through their situation on the dorsal side are exposed to the light most simply and without any torsions being necessary, origin on the ventral side is the best for the roots, and as the whole shoot is pressed to the substratum the position of the twigs upon the flanks is manifestly fitting.

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[1] See with reference to the species of Polypodium—L. Klein, Bau und Verzweigung einiger dorsiventral-gebauter Polypodiaceen, in Nova Acta Acad. Leop.-Carol. xlii. Halle, 1881.

[2] See Warming's account of this family, also my 'Pflanzenbiologische Schilderungen,' ii. p. 331.

[3] The case of Nuphar luteum has been mentioned on p. 85.

Many creeping and climbing shoots exhibit more or less flattening. The causes of this have not been investigated. It is possible, at least in many cases, that light has a share in it. In connexion with the examples brought forward in the Fifth Section it will be shown that where in *roots* a flattening takes place under the influence of light a dorsiventral structure is a consequence. In many cases a flattening of the side of shoot-axes and of roots lying upon the *substratum* evidently results from their pressure upon it when they were still in a juvenile plastic condition, whether this be brought about by negative heliotropism or by other causes. I have elsewhere noticed this feature in many aerial roots of orchids[1], and it also probably exists in the stems of many ferns, for example, in Acrostichum scandens where the illuminated side is also flattened (Fig. 48, *I*). In many ferns the flattening has become hereditary, as in the case of the flat crust-like shoot-axis of Polypodium Schomburgkianum (Fig. 48, *II*) where the shoot-axes protect the roots.

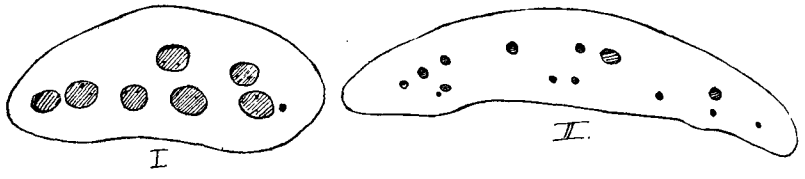

FIG. 48. Transverse sections of two flat dorsiventral fern-stems creeping on the bark of trees. *I* Acrostichum scandens. *II* Polypodium Schomburgkianum.

B. DORSIVENTRAL LATERAL SHOOTS.

If lateral shoots are produced upon an orthotropous chief shoot they often have a dorsiventral instead of a radial construction. This may occur in different degrees and be brought about in different ways, and we may make the following grouping of the latter:—

1. Change of the position of the leaves. This takes place—
   - *a.* By change of the leaf-insertion.
   - *b.* By torsion of the internode or of the leaf-base.
   - *c.* From the beginning at the vegetative point.
2. Different configuration of the leaves upon the upper and under side of the shoot (anisophylly). This is often associated with the changes included under the first heading.
3. Formation of the lateral shoots upon the flanks only of the shoot or preferably there.

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[1] See my 'Pflanzenbiologische Schilderungen,' ii. p. 251.

The chief shoots of our species of oak[1]—Quercus pedunculata and Q. sessiliflora—are radial with a $^2/_5$ phyllotaxy, but their lateral shoots are dorsiventral, for the insertion of the leaves upon them is not transverse but inclines to the long axis of the shoot, in the same way only not so strongly as in the distichous shoots of Tilia, Fagus, and others (Fig. 49). If a shoot be looked at from above, it will be seen that in the leaves upon the left side of the shoot the left margin is deeper than the other, whilst in those upon the right side the right margin is deeper. Leaves which are inserted quite on the dorsal side often show a transverse insertion and the degree of the obliquity of the insertion of the lateral leaves varies greatly. The leaves on the dorsal side of the shoot have also nearly equal sides, whilst on the others the sides of the leaves are differently formed. Anisophylly, about which more will be said presently, is then noticeable in the lateral shoots of the oak and these have passed over in the course of their development from a completely radial primordium to a dorsiventral construction, which however is not strongly marked.

In lateral shoots the leaf-insertions are often brought by torsion of the internode into one plane, which is nearly horizontal. The upper surfaces of the leaves are thus turned towards the light[2]. This is very strikingly the case in shrubs whose leaves are arranged in decussate whorls, such as species of Lonicera, Philadelphus, Deutzia, but it is also found in some which have spiral phyllotaxy, for example, species of Spiraea. I have elsewhere shown[3] that orthotropous shoots which become plagiotropous in feeble illumination from one side exhibit like features, that is to say, a torsion of the internode brings the leaf-surface into a position at right angles to the incident light; Gentiana asclepiadea shows this very clearly when growing at the edge of woods, and it occurs in other plants also. The torsion which brings the leaf-surfaces nearly into one plane is in other cases effected in the leaf-base itself, in the needles of the silver-fir, for instance, but this does not affect the final result. In the Coniferae this phenomenon is connected with the non-development of internodes, and in them the dorsiventral character of the lateral shoots is particularly evident when they branch. The branches of higher order arise exclusively or at least preferably from the *flanks* of the lateral shoots, and in this way the flat branch-system which every one recognizes in the silver-firs comes about. The influence of external factors upon

FIG. 49. Scheme of the insertion of leaves and lateral shoots on the dorsiventral branches of Tilia, Fagus, and others.

[1] See Wigand, Der Baum, p. 45; Mohl, Morphol. Untersuchungen über die Eiche.
[2] See Frank, Die natürl. wagerechte Richtung von Pflanzenteilen. Leipzig, 1870.
[3] Goebel, Zur Morphologie und Physiologie des Blattes, in Botan. Zeitung, 1880.

configuration will form the subject of a later chapter, nevertheless I must here point out how instructive is the difference in behaviour of the spruces[1] and the silver-firs. In the silver-firs the lateral buds on the horizontal branches are all laid down from the beginning upon the flanks alone, occasionally in Abies pectinata and other species they appear also upon the under side of the twig; in the spruces, when they grow strongly in the *open* and are illuminated on all sides, the higher lateral shoots of the chief stem have a radial arrangement of the twigs, the lower ones alone exhibit a development of buds on the flanks, and chiefly those upon the outer side. This is due to the *arrest of the shaded twigs*, that is of *those which arise upon the upper side*, and that this is so is shown by the fact that, so far as I have seen, in spruces grown in *close wood*, branching from the flanks alone takes place also in the higher lateral twigs. Thus here again we see that in one plant outer influences bring about a relationship of configuration which exists in others from the beginning and is hereditary.

As a kind of transition between the two sets of cases just referred

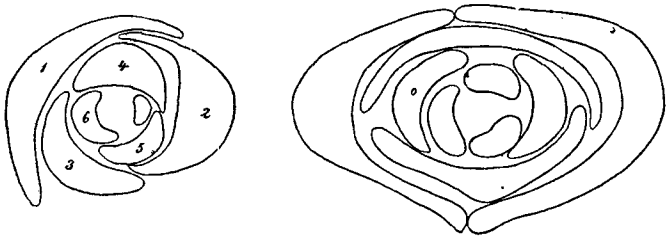

FIG. 50. Vaccinium Myrtillus. To the left a transverse section through the terminal bud of a subterranean stolon; to the right a transverse section of an axillary bud which has developed on a plagiotropous shoot of a plant in darkness; the position of the leaves is not distichous.

to I may now describe the case of Vaccinium Myrtillus (Figs. 50, 51), which I have found to be as follows[2]:—

The seedling of the whortleberry forms at first an orthotropous radial shoot bearing foliage-leaves with a divergence somewhere about $\frac{3}{8}$, but which I have not accurately determined. This shoot has limited growth and its terminal bud is arrested. Lateral shoots arise upon it which develop in part as stolons piercing the ground and bearing only scale-leaves, partly as aerial shoots which are radial like the stolons and have limited growth. The stolons after a time appear above ground and then behave like orthotropous shoots; only their lateral shoots of higher order become plagiotropous and distichously-leaved and produce again shoots which are like themselves. Examination of one

[1] See also Herbert Spencer, Principles of Biology, ii. p. 132.

[2] See also Hofmeister, Allgem. Morphologie, p. 627. I do not find the facts to be altogether as stated by Hofmeister. I cannot agree that the leaves of 'all aerial leaf-buds are arranged distichously.' The behaviour of the orthotropous radial shoot of the seedling shows that this is not so. Compare the analogous case of Lycopodium complanatum, described on p. 103.

of the buds which will afterwards grow into a distichously-leaved shoot shows that its phyllotaxy only gradually passes into the distichous and that the two rows of leaves often exhibit irregularities. First of all the 'prophylls' occur right and left on the lateral bud, enveloping it through the concrescence of their edges (Fig. 51). After them follow two leaves evidently serving as protecting organs and consequently falling away as the bud unfolds, and they are placed as on the bud of a radial shoot, that is to say, almost at right angles to the median plane of the two rows of leaves. The figures show how the distichous arrangement is fully or almost reached in the later leaves, and this takes place, not, as might be supposed, and as I formerly believed[1], by torsion of the internodes, but by a gradual increase of the divergence of the newly formed leaves. Were it produced by torsion the youngest leaves could not stand nearly opposite one another as is often the case. There is here then an *influencing of the vegetative point itself*, which leads to

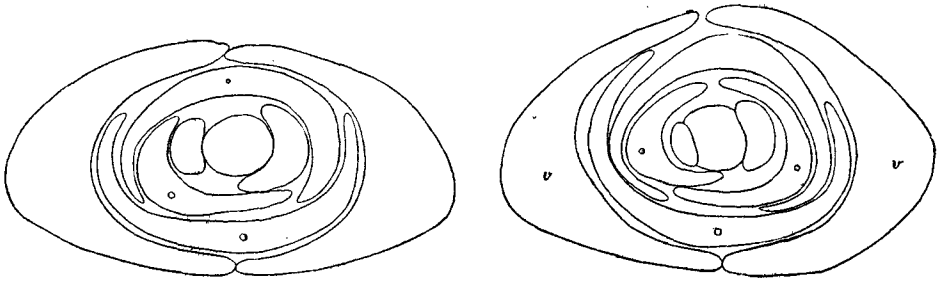

FIG. 51. Vaccinium Myrtillus. Transverse section of two lateral buds in which the distichous arrangement appears after the first four leaves.

a change of the positions of leaves, but this does not take place in all buds alike and is probably brought about by light (see Fig. 50, right).

In other cases a *direct* change in the leaf-position in the course of the development of the individual leaves cannot be proved, or at least has not been proved in those which will be mentioned. Before however proceeding to speak of individual examples it is to be noted that two different things have to be considered in lateral shoots. First of all their plagiotropous position, and secondly their generally feebler formation, in consequence of the influence of the chief shoot and of their position

[1] See Goebel, Entwicklungsgeschichte der Pflanzenorgane, p. 145. The direction of the plagiotropous shoots in the whortleberry is such that they are nearly horizontal in relation to incident light. At the edge of a wood where the illumination is from one side they are erect with the upper surface turned to the light. I may note here that the converse case of a radial ($\frac{2}{5}$) arrangement following upon a distichous ($\frac{1}{2}$) one also occurs, for example in Liriodendron tulipifera, in which the leaves in the bud are arranged with a divergence of $\frac{1}{2}$ and on the expanded shoot have a divergence of $\frac{2}{5}$. See Eichler in Sitzungsb. des Bot. Vereins der Provinz Brandenburg, xxii.

with reference to the earth's radius, which may lead to a diminution of the leaf-rows, altogether apart from the dorsiventrality.

Keeping this in mind, we note the following examples:—In Castanea vesca the leaves stand upon the chief axis of the seedling and upon the stronger stool-shoots in a $^2/_5$ phyllotaxy; on the lateral shoots the phyllotaxy is $^1/_2$. In the seedling of Corylus Avellana the phyllotaxy is $^1/_3$ and the lateral buds of its axis have a distichous phyllotaxy; strong shoots of the hazel, such as are often formed at the base of the shrub, are orthotropous and then show a radial phyllotaxy of $^1/_3$. Species of one and the same genus may behave differently. All the shoots on the European species of birch have a spiral phyllotaxy, but in Betula lenta and Betula nigra[1] only the orthotropous chief shoots exhibit this, the lateral shoots have distichous leaves, and this is also the

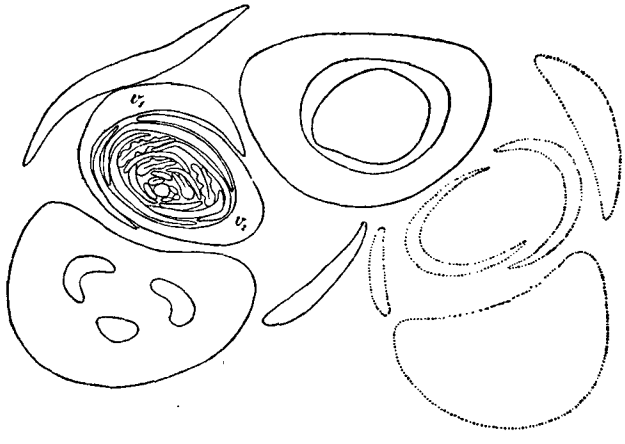

FIG. 52. Tilia parvifolia. Transverse section through a shoot-axis. To the left a leaf with an axillary shoot, v_1, v_2 its prophylls; to the right in dotted outline is indicated the transverse section of a succeeding leaf with its axillary shoot. The leaves converge towards the lower side, but not so strongly as is shown in the figure.

case in Alnus viridis[2]. Analogous cases amongst succulent plants, which are very instructive, will be spoken of in the chapter upon the influence of gravity (p. 219).

If now we imagine the radial chief axis in the trees to which I have referred to be limited only to its seedling state, we should obtain the condition already mentioned as occurring in Carpinus, Ulmus, Tilia, and others which in their later period of growth consist of distichous

[1] See Döll, Flora von Baden, p. 527. Of herbaceous plants Callisia delicatula, one of the Commelinaceae, is the only one I mention here; it has a $^2/_5$ phyllotaxy on the chief shoot and $^1/_2$ phyllotaxy on the lateral ones. The lateral axes show their dorsiventrality in that the leaves are approximated towards the under side and are *oblique*. See Kolderup-Rosenvinge, Undersøgelser over ydret Faktorers Indflydelse paa Organdannelsen hos Planterne, in Vidensk. Medd. Naturh. Foren. i Kjöbenhavn, 1888, p. 57. Other species of Commelinaceae, for example, Cyanotis kewensis, Clarke, behave in like manner.

[2] With reference to Alnus glauca, see Hofmeister, Allgemeine Morphologie, p. 609.

lateral shoots only. Comparison of a number of allied plants convinces us that the radial position of leaves is the primary, and that the distichous must be considered in many plants as a consequence of the lateral position. When we see in one and the same genus, Betula, the lateral shoots in some species distichously-leaved whilst in others they are radial, and in the genus Corylus observe a progression from Corylus Colurna with its radial orthotropous chief stem to Corylus Avellana in which the distichous plagiotropous shoots predominate, it is evident that the extreme case will be that in which, as I have already said, the radial construction is limited to the primary shoot of the seedling whilst all the others show a marked dorsiventrality. We find this in Corylus, Carpinus, Fagus, Ulmus, and Tilia[1], in the position both of the leaves and the lateral buds; the two rows of leaves are not opposite one another but somewhat approximated upon the under side of the shoot-axis; the insertions of the leaves do not run quite transversely to the long axis of the shoot but slightly obliquely (Fig. 49), so that the upper side of the leaf is directed somewhat obliquely upwards and then a torsion of only some 45° at the base of the leaf-stalk is required in order to bring the surface of the leaf horizontal or parallel with the long axis of the twig. The lateral buds do not however stand in the median plane of the leaf but higher up and approaching its upper stipule, just as they do in so many other dorsiventral shoots.

The lateral shoots not infrequently assume a leaf-like habit, and when they do so they also conform with leaves in their limited growth, and like leaves have a joint at their insertion upon the chief axis. The special cases of phylloclades will be referred to in the special part of this book and are not noticed here, but as example I shall take the behaviour of some species of Phyllanthus[2]. In Fig. 53 there is a representation of Phyllanthus mimosoides which shows apparently the bipinnate leaves of many Leguminosae, and from this the specific name has been derived; the same may be said of Phyllanthus lathyroides and others. We have however here really to do with twigs clad with distichous leaves as the fact of their bearing flowers shows. The chief axis and the stronger lateral shoots produce scale-leaves only arranged in a spiral phyllotaxy, and in their axils the smaller lateral shoots arise. I have proved by experiment[3] that in Phyllanthus lathyroides the distichous shoots may be transformed into radial ones so long as

[1] Hofmeister, Allgem. Morphologie, p. 609, includes Aristolochia Clematitis amongst plants in which vertical axes have a $\frac{2}{5}$ phyllotaxy whilst the shoots springing from them at an angle have distichous leaves. I do not know the seedling of this plant, but I find on the orthotropous adventitious root-shoots the $\frac{1}{2}$ position of the leaves *from the beginning*.

[2] Dingler, Die Flachsprosse der Phanerogamen, Heft 1 : Phyllanthus. München, 1885.

[3] Goebel, Über Jugendformen von Pflanzen und deren künstliche Wiederhervorrufung, in Sitzungsber. d. kgl. bayer. Akad. d. Wissensch., xxvi (1896).

they are quite young, and this seems to indicate that they have sprung from radial shoots. Here then, as in Vaccinum Myrtillus, an influence is exerted upon the vegetative point of the lateral shoot.

The examples I have given show that all transitions exist between radial and dorsiventral lateral shoots; in many plants the lateral shoots

FIG. 53. Phyllanthus mimosoides. Top of a plant seen obliquely from above. The radial chief axis of the plant is apparently clad with bipinnate leaves; in reality those are distichously branched leaf-like shoots, the leaves are simple.

are still radial, dorsiventrality is impressed upon them in the course of their development; in others the dorsiventrality already exists in the vegetative point and they cannot usually be artificially transformed into the radial form[1]. Relationships of correlation, speaking of these in the widest sense, and the influence of external forces play an important

[1] See the chapter upon Regeneration, p. 43.

part in this differentiation. Frequently also the chief axis has assumed from the beginning a dorsiventral character as an adaptation, as for example in the ivy, whose climbing or creeping shoots are distichous, whilst the shoots ascending from the substratum and which bear the flowers are radial and exhibit evidently the primary form.

C. ANISOPHYLLY.

By anisophylly we mean that leaves of a different size and of different quality appear on the different sides of plagiotropous shoots; the leaves which stand upon the upper side are usually smaller than those upon the under side, but the converse is also sometimes the case.

Anisophylly is a phenomenon which is repeated in the most different cycles of affinity and also within the same cycle of affinity, even within the same genus, and it appears in different degrees. It will therefore be instructive to follow out some examples taken from different groups. All the examples have this in common, that the anisophylly occurs exclusively upon *plagiotropous* shoots and that it is a *character of adaptation* which has an evident relation to the direction of the shoot and especially to its position with regard to light. This does not mean that light is the determining factor in all the phenomena of anisophylly, for, as will be shown in Chapter II of the Fifth Section, a relationship of configuration does not require to be dependent upon the factor to which it is adapted. The case of Selaginella, which will be mentioned below, shows that anisophylly may appear in a plant in consequence of special circumstances, although the shoots are commonly isophyllous.

Historical.—The striking inequality in the leaves of many dicotyledonous plants has been long known, and has given rise in many cases to specific nomenclature, for example, Goldfussia anisophylla. The brothers Bravais have discussed this plant, and Weddell has excellently dealt with the anisophylly of Elatostemma and other species in his monograph of the Urticaceae. Herbert Spencer in 1865 first directed attention to the anisophylly of lateral shoots in plants with decussate leaves, as well as to the connexion of the anisophylly of higher plants with external factors, especially with light. He says[1]: 'A kindred truth, having like implications, comes into view when we observe the relative sizes of leaves on the same branch, where their sizes differ. Fig. 205 represents a branch of a horse-chestnut, taken from the lowermost fringe of the tree, where the light has been to a great extent intercepted from all but the most protruded parts. Beyond the fact that the leaves are bilaterally distributed on this drooping branch, instead of being distributed symmetrically all round, as on one of the ascending shoots, we have here to note the fact that there is unequal development on the upper and lower sides. Each of the

[1] Herbert Spencer, Principles of Biology, ii. p. 134.

compound leaves acquires a foot-stalk and leaflets that are large in proportion to the supply of light; and hence, as we descend towards the bottom of the tree, the clusters of leaves display increasing contrasts.'

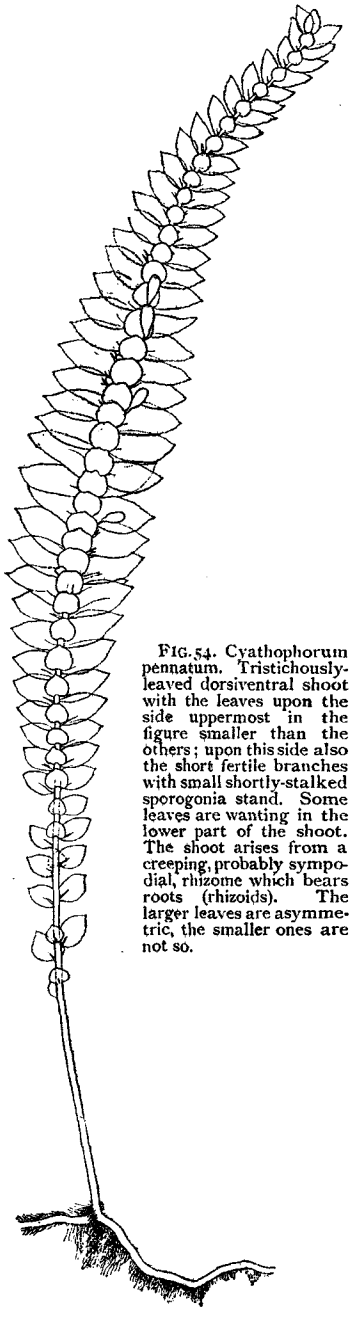

FIG. 54. Cyathophorum pennatum. Tristichously-leaved dorsiventral shoot with the leaves upon the side uppermost in the figure smaller than the others; upon this side also the short fertile branches with small shortly-stalked sporogonia stand. Some leaves are wanting in the lower part of the shoot. The shoot arises from a creeping, probably sympodial, rhizome which bears roots (rhizoids). The larger leaves are asymmetric, the smaller ones are not so.

Subsequently Hofmeister[1], Wiesner[2], and Frank[3] gave attention to anisophylly. The term has come to us from Wiesner, although his definition, which is as follows, is too narrow[4]: 'I mean by anisophylly that the leaves lying upon the upper side of prone shoots have smaller dimensions than those upon the under side, whilst the lateral ones are intermediate.' We know, however, that the leaves on the under side may be smaller, as is the case in the foliose Jungermannieae and in Lycopodium complanatum[5]. I was the first to show in some very striking examples that in habitually anisophyllous shoots we have to deal with *photo-plagiotropy*[6].

The following examples of anisophylly are selected from different groups:

A. MUSCI.

Most of the shoots of the Musci are orthotropous and isophyllous; some of the plagiotropous shoots are isophyllous, for example, in the plagiotropous species of Hypnum. The plagiotropous foliage-shoots of Mnium undulatum[7] (Figs. 28 and 29) usually exhibit an indication of anisophylly inasmuch as the leaves which stand upon the upper side are somewhat smaller than the others, but this is only slightly marked. The anisophylly in Cyathophorum, Racopilum, and Hypopterygium is much more con-

[1] Hofmeister, Allgemeine Morphologie der Pflanzen, 1868.

[2] Wiesner, Beobachtungen über den Einfluss der Erdschwere, in Sitzungsber. d. Wiener Akad. d. Wissensch., lviii (1868).

[3] Frank, Über die Einwirkung der Gravitation auf das Wachstum einiger Pflanzenteile, in Botan. Zeitung, 1868.

[4] Wiesner, Untersuchungen über den Einfluss der Lage auf die Gestalt der Pflanzenorgane, l. c. ci (1892), p. 694.

[5] The cause of anisophylly will be discussed in the Fifth Section.

[6] Goebel, Über einige Fälle von habitueller Anisophyllie, in Botan. Zeitung, 1880, p. 839.

[7] The sexual shoots are orthotropous.

spicuous. A glance at the representation of Cyathophorum pennatum in Fig. 54 will suffice for the recognition of this, and according to the statements in the literature[1] the larger leaves are inserted upon the side which is turned to the light and the smaller ones are upon the under side, as is the case in liverworts. The larger leaves of Cyathophorum, and more so those of some species of Hypopterygium, for example Hypopterygium fuscolimbatum, are asymmetric like those of many dorsiventral shoots of the higher plants; they are divided by the leaf-nerve into two unequally large parts of which the smaller is overlapped, and this again seems to indicate that the smaller leaves lie upon the shaded side. As I have only been able to examine dried material I am unable to say with certainty whether this is always so.

B. HEPATICAE.

Anisophylly and its relation to dorsiventrality and to plagiotropous growth appears in a very striking manner in the foliose ('acrogynous') Jungermannieae. In them the stem clings to the substratum, although I have satisfied myself that they are positively heliotropic in very feeble light; seldomer they are obliquely ascending, as in Mastigobryum.

The shoots have three rows of leaves, two of which are lateral and the third is on the under side composed of much smaller, very often extremely reduced, leaves which are called amphigastria. These leaves are derived from the segments of a three-sided pyramidal apical cell which turns one of its sides to the substratum. In those forms which possess fully developed amphigastria the apical cell has an equal-sided triangular projection, whilst in those which have either reduced amphigastria or none at all the side of the apical cell turned to earth is smaller than the others. The dorsiventrality is then already expressed in the structure of the vegetative point. The lateral leaves are originally inserted transversely to the long axis of the shoot, but they are subsequently displaced so that their upper surface is turned upwards, and their insertion becomes either oblique or comes to be almost in the long axis of the shoot. This however occurs, so far as my experience goes, only in the forms in which the leaves are developed as flat plates; where the leaves have the form of cell-rows the displacement does not take place, for example, in Jungermannia trichophylla and Arachniopsis. Such displacement brings the leaves into a favourable light-position, and, according to my investigations, light is the direct cause of it in many cases. As a consequence of it the lateral leaves have frequently an asymmetric construction, the 'lower lobe' being smaller than the 'upper lobe,' whilst

[1] C. A. Müller, Synopsis muscorum frondosorum, vol. ii. p. 3.

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in the amphigastria, the insertion of which is not changed, asymmetry is not observed, nor is it seen in lateral leaves which are not displaced from their transverse insertion. In the special part of this book the position of the leaves on the sexual shoots in which anisophylly entirely disappears will be discussed. A comparative consideration shows that the dorsiventral construction of the vegetative shoot must be regarded as standing in direct relationship to light. The shoots of Mastigobryum trilobatum which function as 'rhizophores' have three rows of leaves of *equal size* with a *transverse* insertion, and they grow away from the source of light and are not plagiotropic. If one of these be cut off and be allowed to continue its growth in light it will pass over into the ordinary strongly anisophyllous shoot. Other examples show that anisophylly in the dorsiventral liverworts is a secondary phenomenon of adaptation, and this is of importance in the phylogenetic consideration of the group. I may only mention one other instance. Calypogeia Trichomanes has dorsiventral shoots clinging to the surface of the ground, and bearing very small, often reduced, amphigastria. These shoots become orthotropous when they produce gemmae, and then the amphigastria become larger and are hardly less in size than the lateral leaves although previously they were far surpassed by them.

The few isophyllous Jungermannieae are orthotropous, for example, Calobryum and Haplomitrium, but it appears, as I have before now remarked, that Calobryum may become sometimes plagiotropous and at the same time also anisophyllous, as is the case in a species of Selaginella about which I shall presently speak.

C. Pteridophyta

Examples of anisophylly are unknown in the Filicineae and Equisetineae. Its absence from the Equisetineae need not surprise us as the leaves in this class are not assimilating organs and anisophylly stands, as we have seen, in relation to the assimilative capacity dependent upon light. *Heterophylly*, which occurs in many forms and will be spoken of later, does not call for consideration here, as it relates to a *qualitative*, not a *quantitative* difference in the leaf-formation [1].

Some Lycopodineae, however, have to be mentioned here. In some species of the genus Lycopodium, for example Lycopodium clavatum and Lycopodium inundatum, plagiotropous creeping shoot-axes are found, which show indeed, so far as the size of the leaf is concerned, no dorsiventrality but do so in the arrangement of the parts of their vascular bundle-

[1] This is so in the typical cases at least; but anisophylly may also be expressed in qualitative differences in leaves, as will be shown in the case of some Urticaceae.

system and in their cortex[1], whilst the orthotropous shoots of Lycopodium Selago are radially constructed in these respects. Anisophylly appears on the other hand in the cycle of affinity of Lycopodium complanatum (L. complanatum, L. alpinum). In Lycopodium complanatum the plant possesses a subterranean chief axis from which lateral shoots of limited growth pass out into the light. It is not superfluous to remark regarding these Pteridophyta that the subterranean parts have no chlorophyll. The aerial shoots, especially the branches of higher order, are strongly flattened, markedly dorsiventral and anisophyllous (Fig. 55). There are four rows of leaves, an upper, two lateral, and one on the under side; on stronger branches there are more. The lateral leaves, which along with their leaf-cushions (the portions of the leaf-bases 'concrescent' with the shoot-axis) do almost all the work of assimilation, are not only larger than the upper and under leaves, but *have also a different form;* they are flat in their apical part like the leaves of the two other rows but in their basal part they are keel-like (Fig. 56, 1), in other words their configuration shows an approach to the form of leaves met with in Fissidens. The keel which is continued downwards into the leaf-cushion is much richer in chlorophyll upon its upper side than upon its under side, and the whole configuration

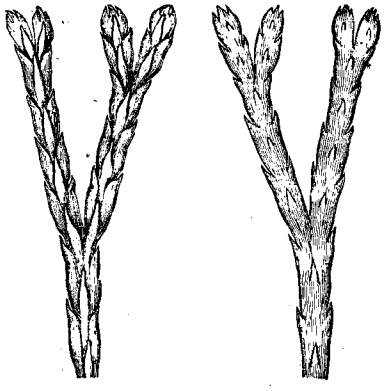

FIG. 55. Lycopodium complanatum. Dorsiventral shoot. The figure on the left shows the side turned to the light; that upon the right shows the shaded side. Magnified about 1½.

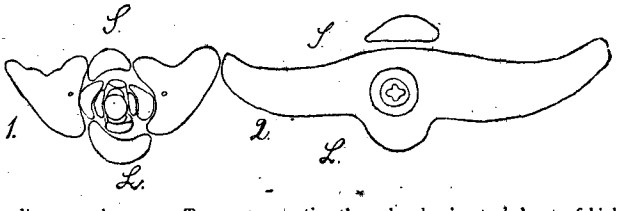

FIG. 56. Lycopodium complanatum. Transverse section through a dorsiventral shoot of higher order; 1 at the apex; 2 lower down. *S* shaded side, *L* illuminated side.

[1] See Hegelmaier in Botan. Zeitung, 1872, p. 776:—The cortex is developed upon the illuminated side into convex ribs descending from the insertions of the leaves, that is to say, leaf-cushions are present, whilst on the shaded side these ribs are wanting, that is to say, there are no leaf-cushions. The strongly dorsiventral shoots of Lycopodium complanatum show the same features in a greater degree (see the text). The species of Lycopodium furnish instructive illustrations of the different degrees in which allied forms may react to external stimuli which influence configuration; what I relate in the text of my investigation of the case of Lycopodium complanatum affords excellent proof of this reaction.

of the lateral leaves evidently fits them to serve most efficiently as flat leaf-like organs of assimilation, without torsion being necessary. The upper and the under leaves are also different from one another. The under ones are smaller, pale, without a prominent leaf-cushion, and take no part in assimilation; the upper leaves are rich in chlorophyll and have a leaf-cushion, and this cushion adds to the assimilating surface although not to any very great extent. The difference in the formation of the leaves is not yet visible in the vegetative point although the dissimilarity between the upper and the under leaves may appear very early (Fig. 56, 1).

The subterranean shoots are very different in configuration from these assimilating shoots. They are radial with spiral phyllotaxy, nearly cylindric in transverse section, bear leaves which are all constructed alike, and have a system of vascular bundles which is radial, whilst that of the dorsiventral shoots is bilaterally symmetric (see Fig. 56, 2). The branching of the subterranean shoots, too, does not take place in one plane, and thus differs from that in the aerial shoots. Between the two forms of shoots there are all intermediate stages. The shoots which raise themselves above the ground only gradually attain dorsiventrality and anisophylly. Primarily they are radial with leaves in many rows; then they flatten upon the side turned towards the light but remain convex upon the shaded side, and the leaves upon the flanks now take on the keel-like form. The branching then proceeds in one plane, and this shows that dorsiventrality is become impressed upon that shoot. Upon the upper parts of the branches thus formed there arise the shoots of higher order described above, which are strongly dorsiventral and have the characteristic arrangement of leaves of this form. My researches have shown that the dorsiventrality as well as the anisophylly is here conditioned by light. In this history we observe then the gradual engrafting of both features, and that shoots of a higher order react more strongly in response to the external determining factor than do those which spring as lateral branches directly from the rhizome; at the same time it is of extreme interest to see how within one cycle of affinity, that namely of the Lycopodieae, the problem of making a shoot with four rows of leaves into a plagiotropous dorsiventral anisophyllous one is solved in different ways. This is accomplished in Selaginelleae by quite other means. In Lycopodium complanatum the four-rowed phyllotaxy arises by reduction; whether such a process takes place in the Selaginelleae we leave undecided, as we have here only to do with observed relationships; at any rate the reduction in the Selaginelleae with four rows of leaves must have taken place only in the course of *phylogeny*, not in the *ontogeny*. The differences in the point which is reached by the same path show us again that in all adaptations we must consider not only the influence of the environment,

but also and particularly the manner in which the plant on account of its material nature responds to this.

The different species of Lycopodium furnish also an illustration of the varying sensitiveness to the influence of external factors existing in one genus. The plagiotropous shoots of Lycopodium annotinum and others are only feebly dorsiventral in respect of the development of their cortex and vascular system. In Lycopodium alpinum the dorsiventrality increases and approaches nearly to that of Lycopodium complanatum; the leaf-cushions upon the illuminated side are in this species more developed than they are upon the shaded side (see Fig. 57), and the

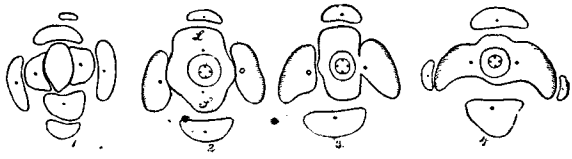

FIG. 57. Lycopodium alpinum. A series of transverse sections through a shoot at different heights, 1 being the highest, 4 being the lowest. *L* the illuminated side is turned upwards, *S* the shaded side is turned downwards. In 2, 3, and 4, the portion of the leaf-cushion which is richest in chlorophyll is indicated by shading.

leaf-cushions of the lateral leaves are strongly flattened and dorsiventral; but the lateral leaves themselves are not so altered as they are in Lycopodium complanatum. They are usually flat and experience a kind of torsion only in their basal portion where it passes into the leaf-cushion, and here they also become feebly keel-like (see Fig. 57); the leaves on the shaded side are more strongly developed than in Lycopodium complanatum. The leaves which are found upon the under side of the feebly dorsiventral creeping shoots of Lycopodium inundatum are also smaller than the others and often have no chlorophyll.

Selaginella. In the extensive genus Selaginella[1] we find both isophyllous and anisophyllous species. The latter, which are the most numerous, possess four rows of leaves, and the leaves of the two rows which are turned to the light are smaller than those on the under side of the stem, but there is one species which according to external circumstances may be either isophyllous or anisophyllous. This is Selaginella sanguinolenta which I have carefully investigated, led thereto by a remark of Spring in his Monograph of the Lycopodiaceae.

This species which usually lives on stony spots[2] and, as we may conclude from its anatomy, in places which are, at least sometimes, dry, possesses erect shoots with four rows of adpressed thick leaves which are

[1] Baker, Handbook of the Fern-allies, enumerates 334 species of which eight are isophyllous.

[2] The isophyllous species of Selaginella usually grow on dryer and brighter spots than the anisophyllous. I at least come to this conclusion from my observation of S. spinulosa and S. rupestris; the adaptation to periodical drying up of species like S. lepidophylla amongst anisophyllous forms is a secondary phenomenon.

all of equal size and are inserted transversely to the long axis of the shoot (Fig. 58). In addition to these shoots there are others exhibiting anisophylly although not in so high a degree as it appears in other species of Selaginella. The leaves of the upper side of these shoots are *smaller* than are the lateral leaves (Fig. 59), and they have an *oblique* insertion which places them in a favourable position to incidence of light without their overlapping one another to any considerable extent. Shoots possessing such leaves grow in shaded and moist situations, and the leaves are larger than they are in the isophyllous shoots as the habitat would lead us to expect. They have become plagiotropous and slightly dorsiventral under the influence of feeble unilateral illumination.

FIG. 58. Selaginella sanguinolenta. Apex of an ordinary isophyllous shoot. There are four rows of equally large leaves of similar configuration.

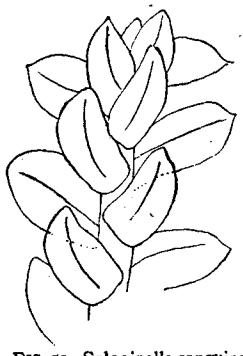

FIG. 59. Selaginella sanguinolenta. Dorsiventral anisophyllous shoot seen from above. Magnified somewhat more highly than is Fig. 58.

The dorsiventral structure which in this species is a direct consequence of external factors is in the other species of Selaginella, so far as we know, inherited, and is independent of external factors. In many species, for example Selaginella caulescens, the shoots are at first orthotropous and completely isophyllous, but subsequently become plagiotropous and anisophyllous; whilst in others the anisophylly appears from the beginning. The lateral leaves turn their morphologically upper surface to the light, those which stand upon the upper side have their morphologically under surface directed to the light. As a consequence of this the four rows of leaves are characteristically placed so that they do not intersect at right angles (Fig. 60). This happens in other anisophyllous plants, as we shall see, and it is an arrangement by which the leaves which are chiefly concerned in assimilation are brought into a favourable horizontal direction. The dorsiventrality is expressed in the vegetative point, for its shaded side is flattened and its outline on cross-section is not circular, but elliptic. In many species of Selaginella *asymmetry* of single leaves

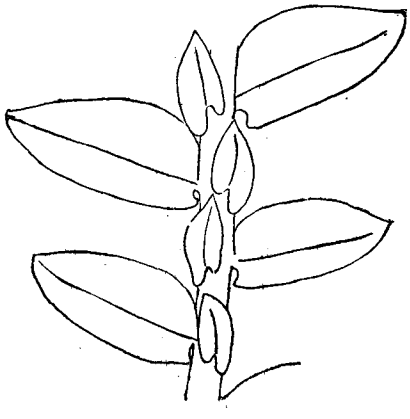

FIG. 60. Selaginella haematodes. Portion of a shoot seen from above. The leaves upon the upper side are smaller than those upon the under side; each leaf also has unequal sides.

appears, and this is also a feature widely spread amongst dorsiventral shoots (see Fig. 61). Whilst then in Lycopodium complanatum two opposite leaf-rows of the four share in the constitution of the assimilating surface, in Selaginella two leaf-rows adjacent to one another are devoted to this purpose; in the former a striking change of *form*, almost amounting to abortion in the leaves of the row upon the shaded side, takes place, in the latter the large leaves are displaced towards the illuminated side whilst they are still in the condition of primordia at the vegetative point,

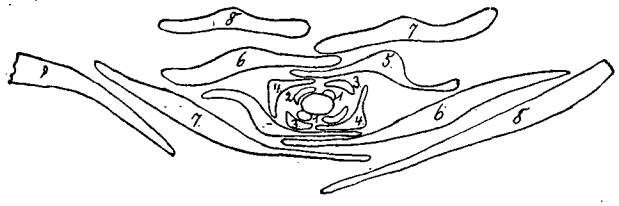

FIG. 61. Selaginella haematodes. Transverse section through the apex of a shoot. The obliquely-crossing leaf-pairs are numbered in the succession of their age. The leaves upon the upper side are smaller than those upon the under side. Leaves 8 and 9 are not entirely shown; in the second and fifth leaf-pair the number belonging to the under leaf has not been put in.

and the two rows of smaller leaves adpressed to the shoot-axis take also a part in the assimilation.

From what has been said, namely—

1. In Selaginella sanguinolenta alone of its genus anisophylly is not constant but appears under the influence of external factors;
2. In many robust species of Selaginella the shoots are still isophyllous in their lower part;

and further—

3. In etiolated shoots of Selaginella helvetica, as I have recently observed, anisophylly has not entirely disappeared but is only retarded[1];

we may learn that in the 'habitually' anisophyllous species of Selaginella we have a phenomenon purely of adaptation brought about by light; the effect of the adaptation is however already visible in the relationships of configuration at the vegetative point. We have also seen examples of this in the lateral shoots (see page 95).

D. SPERMAPHYTA[2].

Anisophylly occurs in different degrees in the same cycles of affinity, and even in the same genus amongst higher plants, just as it does amongst

[1] See also Hofmeister, Allgemeine Morphologie, p. 626.

[2] See, in addition to the literature cited on page 100, Wiesner, Studien über die Anisophyllie tropischer Gewächse, in Sitzungsber. d. Wiener Akad. d. Wissensch., ciii. Abt. 1 (1894); Hallier, Neue und bemerkenswerte Pflanzen aus dem malaiisch-papuanischen Inselmeer, in Annales du Jard. Bot. de Buitenzorg, xiii. p. 279.

lower forms. The leaves of one side, the upper, may be distinguished only by their smaller size from those of the other side, the under, but in extreme cases of anisophylly which are met with in many Urticaceae for instance, Elatostemma, Pellionia, and others, there is not only the difference in size but also a difference in structure and in function between the leaves of the two sides. We may distinguish, although not sharply, two cases—in the one, only the lateral shoots of radial isophyllous chief shoots are anisophyllous, and we may designate this *lateral anisophylly;* in the other, the whole shoot-system is anisophyllous and this may be called *habitual anisophylly.*

a. LATERAL ANISOPHYLLY.

This is seen in most striking form upon the lateral branches of trees and shrubs with large decussating leaves, for example, species of Aesculus, Sambucus nigra, Acer campestre, A. platanoides, A. pseudo-platanus and other species of Acer, species of Fraxinus, Staphylea pinnata; it occurs also in Catalpa syringaefolia which has three-leaved whorls. The differences are less striking where the phyllotaxy is spiral, as for example in Quercus referred to above (page 93), and in Abies which will be mentioned below (page 250).

This anisophylly is not however limited to trees and shrubs but is found in herbaceous plants, for example in Urtica, species of Scrophularia, and others; tropical plants in particular furnish a large number of examples. It is commonly absent from those of our shrubs which, as has been mentioned above, have the leaves of their lateral shoots displaced by torsion into one plane, and if it does occur upon them it is only in the last leaves of an annual shoot which retain their primary position.

We find not infrequently in species of ash and maple that the upper leaf of the pair next to the terminal bud is developed as a bud-scale, whilst the under one of the pair is a foliage-leaf, and this shows that the formation of leaves upon the under side is furthered. In plants with decussating leaves in which the leaf-pairs are not brought into one plane by internodal torsion the leaves either remain in their normal position, that is to say, two rows of leaves are lateral, one row is above, and one row is below, or a torsion takes place by which the four rows of leaves are brought into a diagonal position. In the first instance, which is the common one in lateral anisophylly, the opposite leaves in each leaf-pair of the *lateral* rows are of equal size; in the second case, which always happens in habitual anisophylly, the leaves of the two rows towards the upper side are smaller than those of the two rows towards the under side. In lateral anisophylly however a torsion may also take place, as for example in the horse-chestnut. The larger leaves

have larger axillary shoots than the smaller ones. The advantage of the whole arrangement is evident—the stronger development of the leaves of the under side brings the assimilating leaf-surface more to the periphery of the crown of the tree where the illumination is more favourable [1].

b. HABITUAL ANISOPHYLLY.

The cases to be mentioned here, and only a few can be referred to, link on to that of Selaginella described above (p. 105).

1. Urticaceae [2]. Fig. 62 is a representation of a portion of a shoot of Pellionia Daveauana, and a number of species of Elatostemma

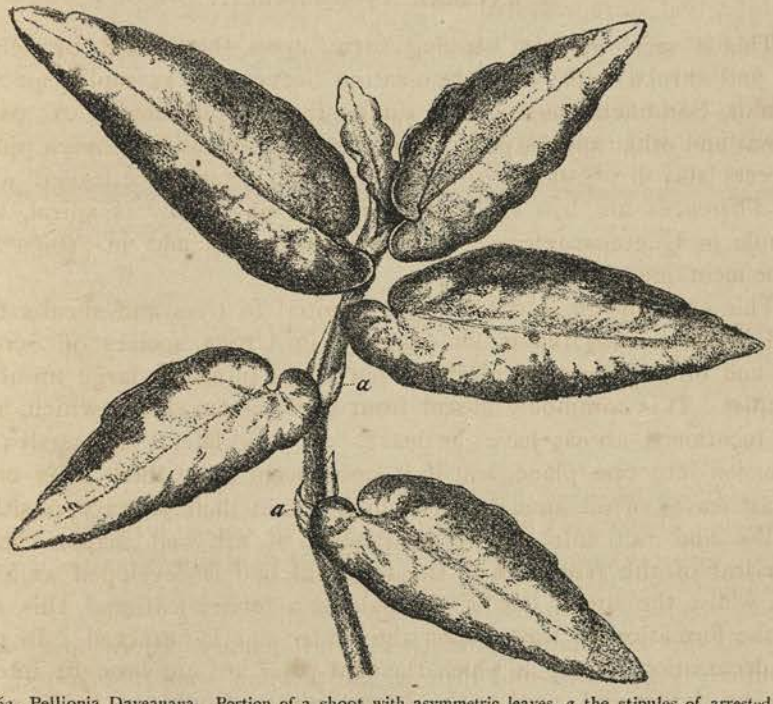

FIG. 62. Pellionia Daveauana. Portion of a shoot with asymmetric leaves, *a* the stipules of arrested leaves which stand upon the upper side. The axillary stipule of the foliage-leaf stands more towards the under side, and the whole appearance is as if each leaf had two stipules.

exhibit features of a like kind. The shoot has apparently two rows of leaves, but there are really four rows, the leaves being in decussate pairs. The opposite leaves in each pair are very unequal in size and

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[1] See the quotation from Herbert Spencer on page 99. Wiesner has termed 'the furtherance of growth of the outer over the inner member of a lateral organ' *exotrophy*; see his Mittheilung über die Erscheinung der Exotrophie, in Ber. der deutsch. bot. Ges. x (1892), p. 552.

[2] See Weddell, Monographie des Urticacées, in Arch. du Muséum d'histoire nat. ix (1856).

unlike in form; the upper leaves indicated by Arabic numerals in Fig. 63 are much smaller than the under ones, but they possess, like them, axillary stipules. In Elatostemma sessile the upper leaves are more reduced (see Fig. 64); there is no longer found here the differentiation which results in the formation of an axillary stipule to the leaf, and the upper leaf itself may be readily taken for an axillary stipule; the under leaves are on the other hand constructed as foliage-leaves, each of which has an axillary stipule serving as a membranous protection to the bud. Fig. 64 represents a cross-section of the bud; the foliage-leaves are indicated by Roman numerals, the small scale-leaves opposite to them by letters; leaf *I* is not indicated, its axillary stipule, st_1, is alone represented in the figure. Opposite to leaf *I* stands the scale-leaf *a* which takes no share in assimilation, and only serves as a protective organ[1]. In

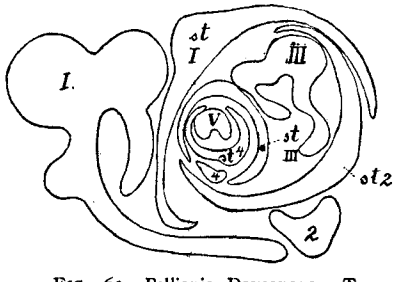

FIG. 63. Pellionia Daveauana. Transverse section of a bud. The larger leaf of each leaf-pair is indicated with a Roman numeral, the smaller with an Arabic numeral. The axillary stipule of each leaf is indicated by *st* with its corresponding numeral. The figure is inverted.

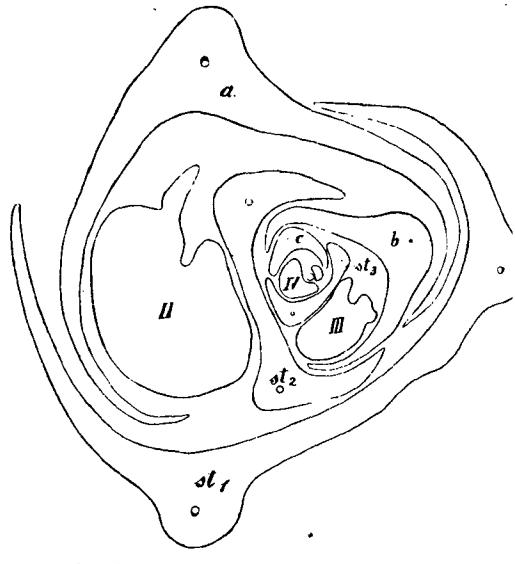

FIG. 64. Elatostemma sessile. Transverse section of a bud. *II–IV* the foliage-leaves (foliage-leaf *I* is only indicated by the axillary stipule st_1); *a*, *b*, *c*, are the opposite leaves of the pairs to which *I*, *II*, and *III* belong and are reduced to scales, and have no axillary stipule.

many species of Elatostemma these rudimentary leaves are said to be entirely suppressed and then a leaf-position would be found, quite like that which is seen in Ulmus. The several species of Elatostemma appear to differ from one another in their whole construction. I observed one species common at Buitenzorg,—I did not identify it,—which was plagiotropous and anisophyllous even on the chief shoot of the seedling; others again I noted possessing a creeping stem from

[1] Weddell regarded this leaf as a stipule. This is an error. It is, although stipule-like, a *leaf* which has been arrested at an early stage of development and has no leaf-lamina. At an early period it becomes covered with hairs like the primordia of the large leaves, and this is a character which the stipules *do not* possess.

which plagiotropous shoots arise with leaves which are equal in size so long as they are in the soil. There are therefore differences like those we find in Selaginella. In Elatostemma sessile, etiolated shoots also show anisophylly. It is quite clear that in all these cases the anisophylly cannot be directly caused by external factors. Vegetative shoots arise only in the axils of the larger leaves, and as these leaves are arranged in two apparent rows on the mature shoots, a flat dorsiventral branching system is developed like that of most species of Selaginella, with which plants Elatostemma has also in common the asymmetry of the leaves. It is easy to find amongst the Urticaceae examples of less marked anisophylly which of course indicate a less degree of biological importance, but I prefer to cite some more examples from other cycles of affinity.

FIG. 65. Centradenia inaequalateralis. The leaves stand in cross-pairs and are very asymmetric. In each leaf-pair one leaf is always much larger than the other, and the larger leaf only has an axillary shoot.

2. Melastomaceae. The genus Centradenia includes species possessing varying degrees of anisophylly. The differences in the leaves are extremely well marked in Centradenia inaequilateralis whose sickle-like leaves are conspicuous on the plagiotropous shoot-system (Fig. 65). The construction of the leaf-shoot evidently points to a shaded habitat for the plant in which it receives the rays of light at a right angle. Centradenia floribunda shows the anisophylly to a less extent, especially on the orthotropous shoots; the larger leaf here has a length of 6 cm. and a breadth of 1·4 cm., whilst the smaller has a length of 5 cm. and a breadth of 1·1 cm. The sickle-like curvature of the leaf is only slightly

indicated in this species. The plant does not form a flat branch-system because the smaller leaves produce axillary shoots; this is the case at least in plants cultivated in plant-houses, but it is possible that in the shade of woods of the natural habitat the plagiotropy and anisophylly may be more marked[1]. In any case these characters are not so fixed here as they are in C. inaequilateralis.

3. Acanthaceae. I take the genus Goldfussia as an example, and Fig. 66 is a diagram of the positions in Goldfussia glomerata. The leaves are in this species decussate, but the leaf-pairs are subsequently displaced so that they do not cross at right angles; the divergence between the larger leaves becomes greater than 90° and they appear displaced to the sides, whilst the divergence of the smaller leaves becomes less than 90°. The axillary buds are shown in transverse section in the diagram. Each of them begins with two lateral leaves of which one is

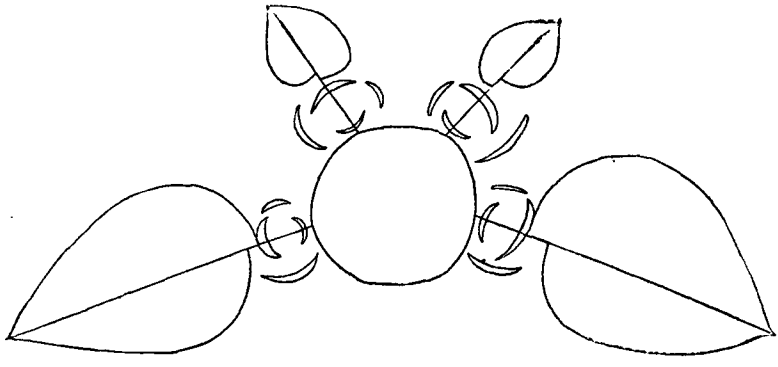

FIG. 66. Goldfussia glomerata. Diagram. The leaves of the chief shoot are seen in surface view, those of the axillary shoot in transverse section.

commonly smaller than the other, and they are followed by a second leaf-pair in which the leaf next the mother-axis is the smaller. This position is of importance, as I have elsewhere pointed out, because it shows that the anisophylly does not stand, as was formerly supposed, in direct causal relationship to gravity. It is true that in the first pair of leaves the leaf which is towards the inner side, when one regards the chief shoot as being inclined or horizontal, is the larger, but in the following pair of leaves, in which the disposition in relation to the mother-shoot is the critical one, this is not the case, but the larger leaf is always that which is on the side of the bract and away from the mother-shoot, no matter whether the bud lies towards the upper side or towards

[1] The differences are often somewhat greater than I have stated and they would seem to be variable. In dried specimens in the herbarium I have found the small leaves only 1-2 cm. long and large ones 4-6 cm.

the under side[1]. At a subsequent period the leaf-rows come by torsion to occupy a diagonal position. Species of Strobilanthus supply other examples of anisophylly in this family.

4. Gesneriaceae. In this family Columnea shows anisophylly feebly in C. Schiedeana, very strongly in C. Kalbreyeri and C. purpurata. It is probable that the two rows of small leaves upon the upper side are suppressed in many Gesneriacae, for example in Klugia, Rhynchoglossum, and others. As a matter of fact I frequently found upon the upper side of the shoot in Klugia a leaf, usually smaller than the lateral leaves, which was evidently a vestige of the upper leaves.

Anisophylly may also appear on sympodial shoot-systems, which, growing plagiotropously, behave like monopodial shoots. One of the best examples of this is supplied by the flowering plagiotropous shoots of Atropa Belladonna, in which the leaves upon the upper side are much smaller than those upon the flanks, whilst the orthotropous chief shoot is isophyllous. The construction of this shoot conforms entirely with that of Selaginella, Elatostemma, and others, although the mode in which it comes about is different.

Reviewing the long series of examples of anisophylly to which we have referred above, we are led to the following conclusions:—

1. Anisophylly appears in different degrees amongst the higher plants and amongst the lower plants, and often in different fashion in one genus.

2. It generally occurs only in plagiotropous shoots, and in the more sharply developed cases appears as an adaptive character which stands in relation to the provision of a surface of assimilation in one plane, or to the projection of the surface of assimilation to the periphery of the crown of a tree; and the leaves which from their position are less suitable for the formation of this surface show a tendency to reduction and may finally entirely abort. This reduction may be caused directly through the position of these leaves especially in relation to light, but it is in the highest degree probable that relationships of correlation also have an important share in bringing it about. It is sometimes the leaves upon the illuminated side, sometimes those upon the shaded side which are reduced, whilst in Lycopodium complanatum the leaves on both of these sides are reduced together. The strong development of the lateral leaves may have to do with the arrest of the others.

[1] I have observed the same positions in the first leaf-pairs of axillary shoots in Goldfussia isophylla, although these have subsequently leaf-pairs with leaves of equal size. The difference in size of the leaves of the median pair may be explained biologically by the feebler illumination to which the leaf next the mother-axis is exposed. This leaf in one instance was 6·5 cm. long whilst the opposite member of the pair was 11·5 cm.; in this example the upper leaf of the first pair was also smaller than the under one. The third leaf-pair lying in the vertical plane also showed, but in a less degree, similar features.

3. I do not mean to say that anisophylly is always directly caused by external factors. It is true that in some cases light and the position to the horizontal produce it, as I shall explain more in detail presently, but in many cases there is no direct relationship to external factors. Elatostemma and Goldfussia glomerata show anisophylly of shoots in their etiolated condition and in every position, although in shoots of G. glomerata growing erect it is less in amount; and in the anisophyllous shoots of Aesculus and others the anisophylly is already induced in the bud and is not brought about in the course of its unfolding.

The formation of organs upon lateral shoots can also be influenced, we must note, by the relationships of these to their mother-shoot, relationships which still require explanation, inasmuch as the establishing of the relationships in space naturally does not give us any explanation of how they have come about. I have already referred, when speaking of the Thallophytes on page 89, to facts bearing on this subject, for example, that in Antithamnion Plumula the short shoots upon the side of a long shoot turned towards another long shoot remain smaller than those upon the opposite side.

IV.

RELATIONSHIPS OF SYMMETRY OF LEAVES.

Leaves are in the great majority of cases dorsiventral. But they may also be bilateral and radial for example in Iris and Juncus, as has been already pointed out. A consideration of these cases belongs to the special morphology of Spermaphyta, here I have only to mention that a radial construction of the leaves, or one approaching radial, may be brought about by late phenomena of growth if there is produced a leaf-surface nearly equally developed in all directions and placed at right angles to the leaf-stalk. This may happen in two ways—either through change of position of the parts of a compound leaf, as, for example, in Marsilia, where the four pinnules are of nearly equal size and radiate from one point; or by the formation of a peltate leaf in which the leaf-stalk is joined to the under side of the leaf-lamina instead of being directly continued into it, as, for example, in Nelumbium and some other dicotyledonous plants. In the latter case the leaves are *solitary* and the lamina is at right angles to the orthotropous stalk. The relationships to the shoot-axis disappear in a leaf of this kind; it is to a certain extent an independent orthotropous and radial structure. Thus we find in Cotyledon Umbilicus[1], the long-stalked leaves of the rosette are

[1] See Herbert Spencer, Principles of Biology, ii.

alone peltate, and in proportion as the shoot-axis elongates in preparation for the formation of an inflorescence the leaves become shorter-stalked, the peltate form disappears, and the ordinary form of leaf, with a lamina continued out of the stalk, is developed[1]. The lamina of leaves of this kind is usually so constructed that its median plane divides it into two nearly equal sides. In orthotropous shoots this median plane which falls in the midrib and stands at right angles to the surface of the leaf is one vertical to the horizon. The symmetry of the sides of the leaf is however in reality only approximate.

Neither in the configuration of the outline nor in the arrangement of the venation of the leaf is complete symmetry anywhere met with. The development of the leaf of a fern or of a moss, for example, shows from the outset an unequal construction of the two sides of the leaf[2]. Similarly in the leaf of a dicotyledonous plant with feathered venation, the corresponding nerves on the two sides of the leaf are only seldom opposite one another. Apart from this general absence of complete symmetry there are some cases which require special notice, in which the *asymmetry* of the leaf is extremely marked, and is a *constant* character of the plants in question[3]. Asymmetry occurs most abundantly in foliage-leaves, and in them can almost always be brought into connexion with their biological relationships and especially with their *position*, using this word in the widest sense; but asymmetry is frequent also in cotyledons, prophylls, and bracts. In some plants the cotyledons only are asymmetric, the other leaves are not so, for instance in species of Geranium and Polygonum; whilst in others only the foliage-leaves and not the cotyledons show asymmetry. The following are some examples:—

1. COTYLEDONS.

Examples of asymmetry in these are found in Geranium pratense and other species, Erodium, Lupinus, Astragalus, Cicer, Tetragonolobus, Desmodium gyrans, Polygonum Fagopyrum, and others. We may acquiesce with Lubbock[4] in regarding the inequality in the sides of the cotyledonary leaves as a consequence of their position in the seed

[1] Quite other relationships obtain in the shorter-stalked peltate leaves of some epiphytic Hymenophyllaceae. For an account of these see the pages upon the configuration of the leaves of ferns in Part II of this book.

[2] See what is said on this subject in Part II of this book.

[3] See the account by Wydler, Über asymmetrische Blätter und ihre Beziehung zur Symmetrie der Pflanzen, in Flora, 1857, p. 209; Herbert Spencer, Principles of Biology, ii. chap. ix.; Wiesner, Untersuchungen über den Einfluss der Lage auf die Gestalt der Pflanzenorgane: I. Die Anisomorphie der Pflanze, in Sitzungsber. d. Akad. Wiener, 1892, and other communications of the author cited there.

[4] Lubbock, A contribution to our knowledge of seedlings, vol. i. p. 34. London, 1892.

and of the configuration of the seed; it is not a phenomenon of adaptation. In Fig. 67 we have a representation of a cross-section of a seed of Geranium pratense. The two cotyledons are so folded that the smaller side of one is invested by the larger side of the other, and the arrest of the one side of each cotyledon is evidently caused by its having less room available than the other[1]. More will be said about this in the section dealing with the development of seeds.

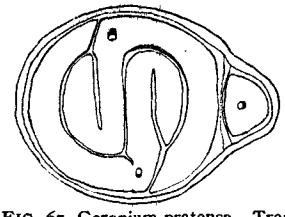

FIG. 67. Geranium pratense. Transverse section through a seed. To the right the hypocotyl; to the left the two cotyledons. The midrib of the cotyledon is evident and it is clear that the inequality of the sides of the cotyledons bears a relation to the available room within the seed-coat.

2. FOLIAGE LEAVES.

We have to consider here both the asymmetry of the entire leaf and the asymmetry of lateral pinnules.

a. ASYMMETRY OF ENTIRE LEAVES.

To this category belong, in the first place, the leaves of a number of plagiotropous shoots, for example those of many grasses, of Columnea Schiedeana and C. Kalbreyeri, of the juvenile form of Ficus stipularis, of the Urticaceae mentioned on page 109 (see particularly Fig. 62, representing Pellionia Daveauana), and of Centradenia; also the leaves of a series of shoots which are not plagiotropous, for example the pendant sickle-like leaves of Eucalyptus globulus, and the leaves of Rochea falcata[2], which differ from most others in that the like-formed sides of the leaves in each pair fall upon opposite sides of the median of the pair (Fig. 68)—in the terminology of Wydler the leaves are 'antitropic'—whereas the similar sides of the leaves in a pair, whether they be the small or the large, usually fall upon the same side.

We cannot doubt that asymmetry of the leaves chiefly appears when 'their parts are unsymmetrically related to the environment[3].' The median plane of such leaves is usually oblique to the horizon—to use Wiesner's terminology they are 'klinotropic'—and the asymmetry stands in connexion with the obliquity of this plane. It is not easy however to determine the factors which condition this, and I must refer to a few examples which may give us a starting-point for the solution of the question.

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[1] The asymmetry in the leaves of many species of Musa may be explained in the same way.

[2] The leaf-pairs of Rochea falcata cross each other at an oblique angle, and this is seen in even higher degree in Mesembryanthemum. The biological significance of these relationships of configuration in Rochea is still unknown.

[3] Herbert Spencer, Principles of Biology, ii. p. 143.

I have already pointed out that in some Commelinaceae the chief shoot is radial, the lateral shoots are dorsiventral. In Callisia delicatula the radial chief shoots have a $\frac{2}{5}$ phyllotaxy and symmetric leaves, the lateral shoots have alternating asymmetric leaves. The leaves of the plagiotropous twigs of the lime are with few exceptions more or less asymmetric, but in cuttings placed erect in the soil Herbert Spencer found a considerable percentage of the leaves quite symmetric. In the elm and the beech the proportion of asymmetry in the leaves varies, but radial shoots of seedlings have always symmetric leaves. On the plagiotropous shoots the leaf which stands at the end of the shoot always has its median plane at right angles to the horizontal, and is not infrequently almost symmetric[1], inasmuch as both sides of the lamina extend nearly equally far down the petiole, whilst in the asymmetric leaves the lower side (directed to the base of the shoot) extends further down the petiole than does the higher.

The asymmetry is then in these cases not strongly inherited, and can be changed by external influences. I do not doubt that it exists in all leaves primarily in a small degree, and is increased in many cases through external influences of which light and not gravity is the chief. The following instance, which I mention here although it rightly belongs to another section of this book, may be taken as an illustration of how, in many cases, light can influence directly the form of a leaf.

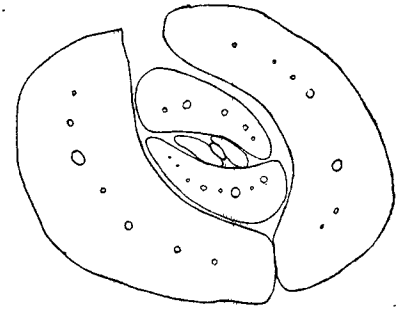

FIG. 68. Rochea falcata. Transverse section through the terminal bud of a seedling. The leaf-pairs are obliquely crossed and the leaves are asymmetric.

In Trichomanes Hildebrandti[2] the leaves stand apparently in one line upon the back of the rhizome which creeps on the surface of the stems of trees; they are sessile and peltate, and their under sides bear hair-roots by which they cling closely to the substratum. *Wherever one leaf is overlapped by another* its growth soon ceases, and the further development of the overlapping leaf is at the points of overlap retarded, and in this way irregularities in the development arise. Observation of the living plants can alone determine with certainty the influential factors here, but it is fair to assume that in the overlapped leaf shading arrests the growth of the leaf. Whether the arrest of growth in the overlapping leaf is to be ascribed, as Giesenhagen has it, to the fact of its

[1] See Wiesner in the papers cited in the note on p. 115. Wiesner, founding on a remark of Hofmeister, assumes that the symmetric leaf at the end of the shoot has arisen from an asymmetric primordium, but in the absence of developmental proof I doubt this.

[2] See Giesenhagen in Flora, 1890, p. 450.

being shut off from the substratum, must remain for the present undecided. The peltate form of the leaf allows of the substratum all round being used, and protects the stem and its buds.

Reverting to the asymmetric leaves[1] we have to remark as follows regarding the disposition of the sides of the leaf:—

The disposition of the sides of the leaf is not always the same in the species of one genus. In the case of a climbing shoot with two rows of leaves and the leaf-laminae all in one plane, as for example in Pellionia (Fig. 62), the large sides in one plant may be turned to the apex of the shoot, in another they may be turned away from it. The genus Begonia has been somewhat carefully examined, and I shall discuss its whole relationships of growth in a few examples.

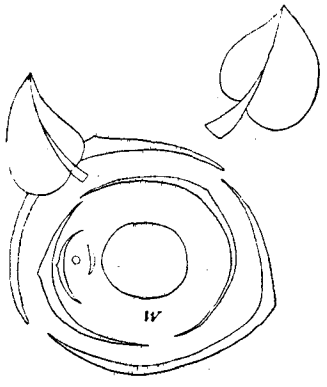

FIG. 69. Begonia Rex. Scheme of the arrangement of the leaves and the branching seen from in front. *W* root-side of the shoot-axis which is shown in cross-section above *W*. In front of each leaf are two stipules seen in cross-section, whilst the leaves themselves are shown in surface-view. In the axil of the second leaf, apparently in that of the lower stipule, there is an axillary shoot.

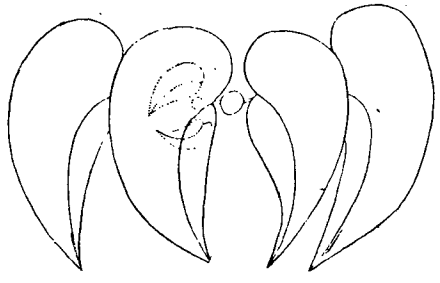

FIG. 70. Begonia incarnata, and others. Scheme of the formation of the leaves and the branching seen from in front

Of course I can only deal with the more general dispositions, for the configuration and the biological relationships of the species of Begonia are manifold.

The genus is distinguished by producing exclusively dorsiventral shoots in the vegetative region, and this dorsiventrality expresses itself in the form of the leaves and of the stipules, and also in many species in the *position* of the leaves and lateral shoots. All species of Begonia have a distichous phyllotaxy and more or less asymmetric leaves, but there are many variations. If we look from the front at a shoot of a Begonia which has grown obliquely, placing it in a horizontal position so that its under side is accurately below, and its upper side is directed

[1] I may remark here that it does not follow that light is the sole exciting factor in asymmetry of leaves because the phenomena stand in relation to light; what I have said above regarding cotyledons shows that *various* external factors may induce asymmetry.

accurately upwards, we shall find upon consideration of the disposition of the unequal sides of the leaves that there are two cases [1]:—

1. In thin-stemmed species, as for example Begonia scandens, B. maculata, B. incarnata (Fig. 70), the *larger* sides of the leaves are directed upwards as in Pellionia, and of the two stipules, which are of unequal size, that which stands upon the illuminated side where it is overlapped is the larger, whilst that upon the shaded side is the smaller.

2. In other species, especially thick-stemmed ones like B. manicata and B. Rex, the *smaller* sides of the leaves are directed upwards and we have the converse of the former case; but in the process of unfolding of the bud a turning takes place by which the leaf-apices, and therefore the smaller sides of the leaves, come to look downwards. In the erect or obliquely ascending species the leaves stand in two rows with a divergence of about 180°, the lateral buds being in the axils of the leaves, but in creeping stems the two rows of leaves approach one another upon the upper side, as is shown in the diagram in Fig. 69, and the lateral buds then stand upon the flanks, and there each of them appears in the axil of one of the stipules—an arrangement the advantage of which is evident, and which is repeated in many dorsiventral shoots.

The disposition of the plane of symmetry of the lateral shoots to that of the chief axis varies. In many cases it falls at right angles to it, and this which predominates in the thin-stemmed species appears to me to be the 'typical' case; in other species the planes of symmetry intersect at a less angle or may indeed coincide [2].

With regard to the biological significance of the oblique construction of the leaves in Begonia, we may say in general with Herbert Spencer [3] that that side of the leaf is the smaller which is shaded, and that the obliquity of the leaf is occasioned by its fitting itself to utilize the space at its disposal; this however does not explain teleologically the difference in size of the stipules; there is indeed accompanying the plagiotropous growth of most species (some of which have again become orthotropous) an inequality in the formation of the sides of the leaves which in many, but not in all cases, appears to have a definite aim.

Species of Begonia which have erect shoots possess, so far as my observation goes, a bushy richly-branched habit. On examining a shoot from above (see Fig. 70) we observe that the horizontal leaf-surfaces

[1] As the result of investigation of a number of species I can confirm what Sachs says in his text-book, p. 209, regarding the relationships. Hofmeister's account is erroneous in more than one point.

[2] See Kolderup Rosenvinge, l. c. on p. 70. Sachs and Eichler differ from Rosenvinge and do not themselves agree. Sachs makes the angle of intersection in thick-stemmed species an acute angle, Eichler in his diagram figures it as obtuse. According to Rosenvinge the plane of symmetry of the lateral buds of B. hydrocotylifolia has the position assigned to it by Sachs, but in B. Rex it is vertical from the beginning (see Fig. 69).

[3] Herbert Spencer, Principles of Biology, ii. p. 144.

are chiefly disposed to one side which we may call the outer side; the leaf-apices do not stand opposite the points of insertion of the leaves, as is usual in shoots with distichous leaves, but the leaves are twisted on themselves through as much as 90°. The dorsiventral character appears then in the erect forms, in that each shoot has an outer side with much leaf-surface, and an inner side with little leaf-surface (the latter is that turned upwards in Fig. 70). As now the individual shoots turn their inner sides to one another, there is developed a shoot-system in which the leafage is *directed outwards*, whilst at the same time the individual leaves are so placed that the shaded side is less developed than the unshaded. I regard this as an instance of 'exotrophy.'

It may be stated as a general rule, that species of Begonia which have short internodes have long-stalked leaves, and the converse is also true, at least in the large-leaved forms. A careful investigation of the biology of the different species in their native habitat would be of the greatest interest, because their conditions of life are so variable. Some are root-climbers like the ivy, for example Begonia scandens, B. fagifolia, and others; others again, like B. Rex, have thick rhizomes growing on the soil or rocks, whilst again others have orthotropous shoots. Leaving aside the climbing forms we might compare the relationships of symmetry in the species possessing elongated internodes (Fig. 70) with those observable in compound leaves with asymmetric leaflets[1], and the shoot-axis of Begonia would then correspond to a petiole and the single leaves to the leaflets.

Asymmetric leaves are found also on orthotropous shoots in other plants, and it is probable that there, just as in the species of Begonia, we have to do with an arrangement for bringing the leaf-surfaces towards the outer side. Thus in Achimenes, one of the Gesneriaceae, which possesses two-membered or three-membered leaf-whorls, the asymmetry of the leaves is as in other species of Gesneriaceae not always, but occasionally, conspicuous, and the leaves have a sickle-like curvature, like that shown in the Begonia represented in Fig. 70. In a garden plant of Achimenes Haageana which I examined, the shoots developed from tubers stood crowded together and were anisophyllous, inasmuch as the leaflets turned inwards were smaller than those standing towards the outside, and the effect of the sickle-like curvature of the leaf-laminae was to bring the leaf-surfaces more towards the outside.

Inequality in the sides of compound leaves is also met with, and it is brought about by the unequal development in size of the leaflets. This may go to such lengths that some of the leaflets on one side of the leaf may be aborted. We may first note that the stipules in many

[1] Of this more will be said below.

dorsiventral Leguminosae are larger upon the upper side, that of the inflorescence, than they are upon the under side. But the inequality of the leaflets is much more conspicuous in a number of species which, so far as I have been able to examine them in the living state, are all distinguished by the possession of markedly plagiotropous prostrate shoots. These shoots have two rows of leaves and one side of each leaf is turned upwards, the other is turned downwards. The differences here are sometimes so prominent that they have found expression in systematic terminology, and we find the leaves of Indigofera diphylla (Fig. 71, *II*), of Hosackia subpinnata, and of Anthyllis tetraphylla (Fig. 71, *III*), described as 'unilaterally pinnate.' In Indigofera diphylla only one pinnule is present on the upturned side. Anthyllis tetraphylla has two to three large leaflets upon its upturned side, and only one pinnule upon the side downwards directed. The leaves are inserted obliquely on the prostrate shoots so that their upper surfaces are directed obliquely towards the upper side of the shoot. Here we have a case of dorsiventrality quite like that of Begonia, and, as in that genus, the sides of the leaves in the plagiotropous shoots which are reduced are the ones that are feebly illuminated. This phenomenon occurs independently in different genera amongst the Leguminosae. I have met with it specially in some Sicilian species. Hedysarum capitatum is very instructive (Fig. 71, *I*), for in it the leaves of the radial orthotropous leaf-rosette are symmetrical and each leaf bears right and left many equal pinnules; but in the prostrate plagiotropous shoots which subsequently develop, one or two leaflets are absent from that side of the leaf which lies next the soil. The same may be seen in Vicia Cracca, in which plant also the stipules standing upon the upper side of the shoot are larger than those upon the under side. Hymenocarpus also (Fig. 71, *IV*) has asymmetric leaves; and a long series of instances might be quoted. The smaller side of the leaf is partially covered by the lateral shoots or axillary inflorescences if these be present. In Anthyllis tetraphylla I found that the small pinnules which have a tendency to abortion possess an anatomical structure different from that of the large terminal

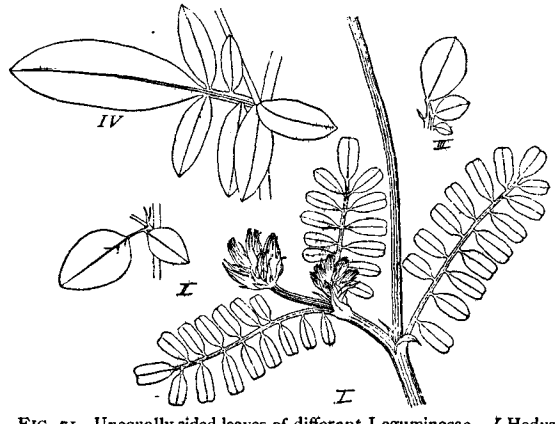

FIG. 71. Unequally-sided leaves of different Leguminosae. *I* Hedysarum capitatum; *II* Indigofera diphylla; *III* Anthyllis tetraphylla; *IV* Hymenocarpus circinnatus.

leaflet; they are only half as thick, and they have either no evident palisade-cells, or only a series of quite short palisade-like cells, whilst in the terminal leaflet there are two rows of palisade-cells. In other words, their structure reminds one of that in shaded leaves, and this gives support to the view that the reduction or suppression is a result of the hinder side of the leaf occupying a position in which it receives less light than the fore side, chiefly because it is covered by the sides of the axillary shoots.

b. ASYMMETRY AND UNEQUAL SIZE OF LEAFLETS.

We have here to speak of two kinds of relationships—(*a*) firstly of the *asymmetric construction* which appears in many leaflets, and (*b*) secondly of the *unequal construction of the single leaflets* of a compound leaf which *does not cause asymmetry* of the whole leaf.

a. ASYMMETRY OF LEAFLETS.

We frequently observe in compound leaves that the terminal leaflet is symmetric whilst the lateral leaflets are asymmetric. From the large number of examples I select the following: species of Rubus, species of Tetragonolobus and Phaseolus amongst Leguminosae, Juglans, Chelidonium, Fraxinus, Heracleum—plants it will be noted of the most different cycles of affinity. Using the term 'higher' for that side of a leaflet which is directed to the point of the leaf we find that it is the lower side, seldom the higher, which is the larger; see, for example, Cedrela amara, Caesalpinia Sappan, Tamarindus indica—plants which I mention here because I have them before me in a living condition. De Candolle[1] has expressly stated that in asymmetric leaflets the lower side is always the larger, but what I have said shows that this is not quite correct. Hofmeister has endeavoured to trace the asymmetry of lateral leaflets to a unilateral influence of gravity. He says[2]: 'The lateral leaflets of many compound leaves both pinnate and digitate show an evident superiority in the outline of the lower side of the lamina over the higher side. If such compound leaves have a terminal leaflet its sides are equally developed. As examples we have Pavia macrostachya, Aesculus Hippocastanum, Ptelea trifoliata, Staphylea trifoliata, Rosa pomifera and R. gallica, Sorbus Aucuparia, Rubus Idaeus and R. fruticosus, Pterocarya caucasica, Robinia viscosa, Cytisus Laburnum, Gleditschia

[1] De Candolle, Organographie Végétale, i. p. 346.
[2] Hofmeister, Allgemeine Morphologie, p. 592.

horrida, Sophora japonica, Vitex Agnus-castus.' The relationships of position of the leaflets within the bud may be most different, and consequently an influence of gravity cannot exist. 'A careful investigation shows however that a difference in the size of the sides of the leaflets in the closed bud does not exist in all observed cases; no marked constant difference, nor indeed any difference at all, in the breadth of these sides can be shown (established in Vitex, Staphylea, Rosa, Pterocarya . . . .). The difference in the growth of the sides of the leaflets only appears whilst the unfolding of the bud is going on, and during this the side of the leaflets which subsequently is least developed is always the higher with its edge turned towards the zenith.'

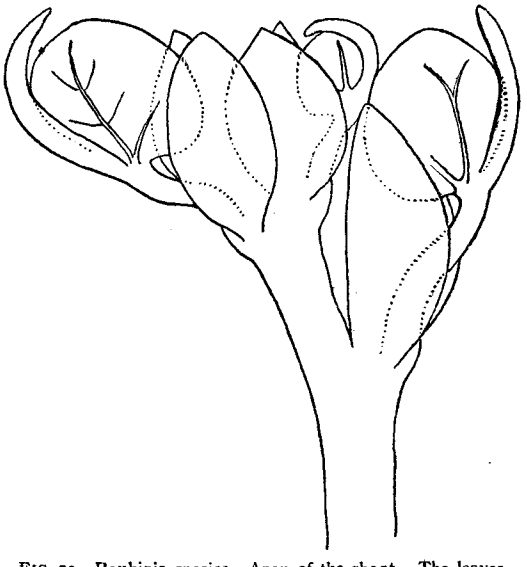

FIG. 72. Bauhinia species. Apex of the shoot. The leaves have two leaflets strongly asymmetric from an early period; at the base of each leaf are two stipules.

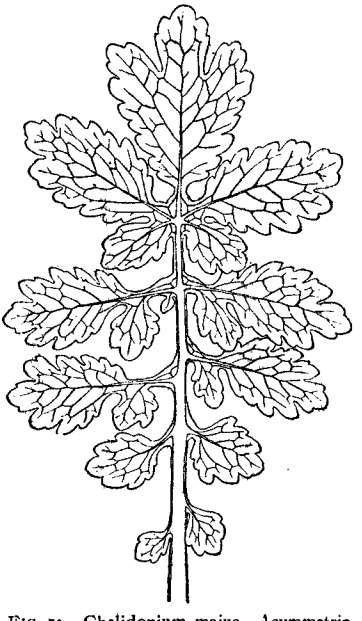

FIG. 73. Chelidonium majus. Asymmetric configuration of the leaf-lobes. Reduced about half.

I have no doubt whatever that this view is altogether untenable; what is stated in the last sentence is not founded upon fact. I agree with Spencer when he says[1]: 'How far such differences of development are due to the positions of the parts in the bud; how far the respective spaces available for the parts when unfolded affected them; and how far the parts are rendered unlike by unlikenesses in their relations to light; it is difficult to say.' The features exhibited by the species of Bauhinia represented in Fig. 72 permit us to assume that an

[1] Herbert Spencer, Principles of Biology, ii. p. 139.

influence may be exerted by the lie of the leaves in the bud. Its leaflets are strongly asymmetric and the asymmetry appears very early, long before the unfolding of the bud. This is quite opposed to Hofmeister's statement. The higher edge of the leaf is covered and protected by the aborting end of the leaf, the lower edge lies free between the stipules, which close upon it like the shell of a mussel, and it is in relation to this perhaps that we have the feebler construction of the upper sides of the leaflets. Herbert Spencer has already shown that in other cases it is the smaller side which is in a favourable position to utilize the light inasmuch as it avoids shading. There is however no case known up till now in which it has been possible to hinder or to bring about asymmetry experimentally.

The formation of the leaf of Chelidonium majus I shall briefly mention here because it is very instructive (see Fig. 73). The terminal

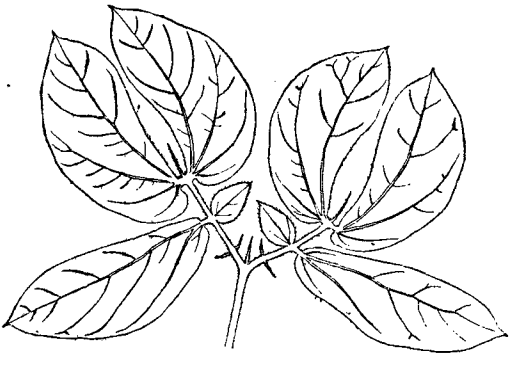

FIG. 74. Mimosa sensitiva. Leaf. At the base of each of the two chief pinnules are two 'stipelles' (reduced pinnules of the second order). Natural size.

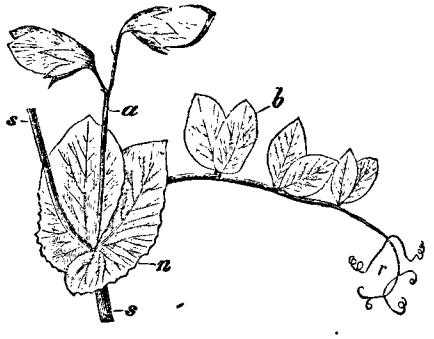

FIG. 75. Pisum sativum. Portion of a shoot. The stipules *n* of the pinnate leaf are strongly asymmetric. Lehrb.

leaflet and the lowermost lateral leaflets are nearly symmetric and the latter stand out at an angle of about 45° from the midrib of the leaf. The higher lateral leaflets are strongly asymmetric, the lower side-lobe of each being strongly developed. In correspondence with this projection the higher side of each of the adjacent leaflets exhibits an indentation at the place upon which in illumination from above the shade of this lobe would fall. The individual leaflets are moreover not spread out in the plane of the terminal leaflet but make an angle with it; and the lowermost leaflets by their oblique position escape the shadow of the higher ones. If, as in other cases, we refer this construction teleologically to a relationship with light, we have to admit that we do not know anything as yet about its origination.

The leaf of Mimosa sensitiva, represented in Fig. 74, supplies an illustration of a compound leaf on which one of the leaflets of a pair

is symmetric whilst the other is asymmetric. The leaf is bipinnate; the terminal lobe is aborted and the lateral leaflets are of very unequal size, the larger being strongly asymmetric, the smaller nearly symmetric. The relationships of symmetry find an easy teleological explanation here; if in the asymmetric leaflets the smaller side was as large as the larger, overlapping would take place; the smaller and inner leaflets have only to fill up the interval between the larger.

We are naturally led from a consideration of plants with asymmetric leaflets to those in which the *stipules* are asymmetric. This is the case in many Leguminosae, for example species of Vicia, Pisum (Fig. 75), Orobus, and Lathyrus, and also in Rosaceae, for example in Spiraea Ulmaria, Agrimonia, and others. We know nothing of the factors which cause the asymmetry here, and can only bring it into relationship on the one side with the position of the stipules, and on the other with their function. It is usually that portion of the stipule which is *turned away* from the leaf, in which the stronger growth is observed, and thus the protection of the bud is favoured. Lathyrus Aphaca is interesting in this respect (see Figs. 76 and 77), inasmuch as the stipules of the fully-formed leaves are asymmetric whilst those of the arrested or the tendrillous leaves are symmetric. The unilateral increase in the configuration of the stipules will be understood in its teleological relation by a glance at Fig. 78, which shows a transverse section through the bud of Vicia Cracca. The leaves here are in two rows, as in other Leguminosae, and are folded from the midrib, and each leaflet is similarly folded. As the leaves are very hairy upon the outer side the bud is well protected. Above and below however there are two longitudinal strips which are covered by the *stipules*, st_1–st_6, and it is clear that the protection they afford to the bud will be all the better the more they are extended on the sides which are directed away from the leaves, because places occur there which are not protected by the leaves themselves. This unilateral growth takes place, if some observations on Lathyrus sativus enable us to judge, only relatively late, the stipules are primarily laid down as symmetric structures. When the leaf itself, as in Lathyrus Aphaca (Fig. 77), takes practically no share in the protection of the bud, the stipules must take on the whole of this duty, and we can at least teleologically understand that asymmetry is a consequence; and the fact that its development only takes place at a relatively late period gives support to the assumption that the asymmetry is only a secondary character of adaptation.

b. LEAFLETS OF UNEQUAL SIZE.

Mimosa sensitiva supplies an example of the different development of the leaflets of one and the same leaf[1]. This feature appears

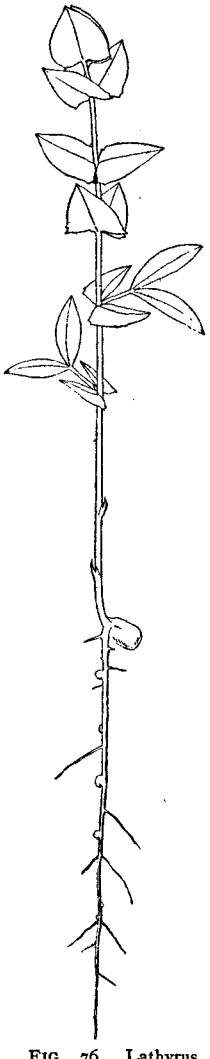

FIG. 76. Lathyrus Aphaca. Seedling. The stipules of the two lower leaves in which the leaf-lamina is formed are asymmetric, but those of the upper leaves in which the leaf-lamina is arrested are symmetric.

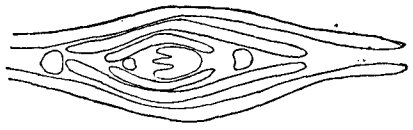

FIG. 77. Lathyrus Aphaca. Transverse section through the shoot-apex. The large stipules alone protect the bud.

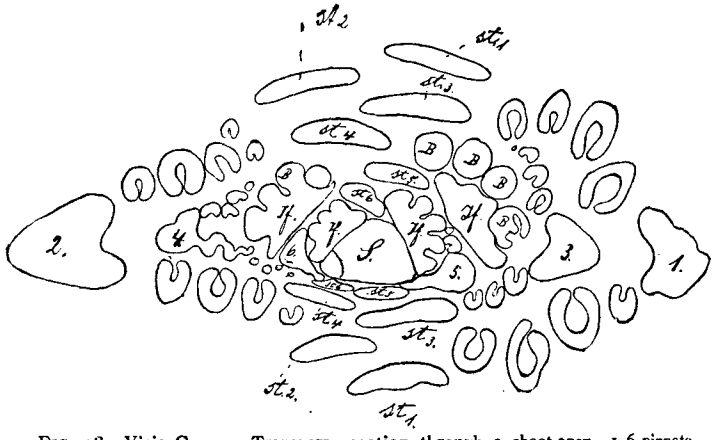

FIG. 78. Vicia Cracca. Transverse section through a shoot-apex. 1-6 pinnate leaves, the stipules st_1–st_6 of which fill up the space both above and below between the leaves and so protect the bud. See also explanation of Fig. 83.

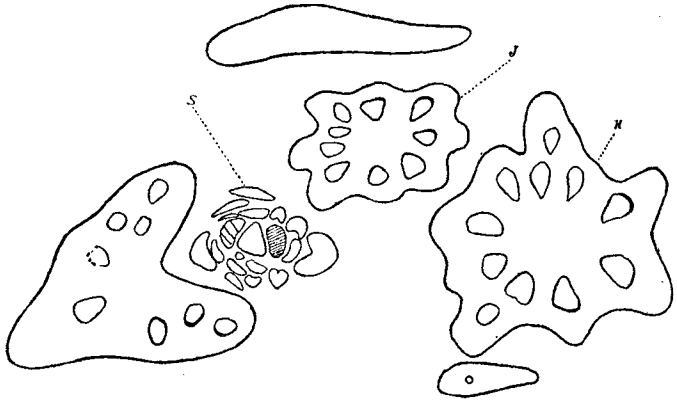

FIG. 79. Vicia Cracca. Transverse section through a chief axis *H*. In the axil of the leaf to the left stands the inflorescence *J*, and below it is the accessory shoot *S*, which has also already produced axillary inflorescences indicated by shading in the figure. The plane of symmetry of the shoot *S* is almost parallel with that of the chief shoot. The inflorescences in both are displaced towards the illuminated side.

[1] We leave out of account the smaller differences in size which frequently occur and are due to the later-formed leaflets not reaching the dimensions of the earlier ones.

in the leaves of plants in very different cycles of affinity, for example in all those which are designated as 'interruptedly pinnate,' such as Solanum tuberosum, species of Geum (see Fig. 81), Potentilla anserina, Spiræa Filipendula, and others. In all these plants individual leaflets lag behind others in their growth, and an advantageous arrangement for making the best use of the light is by this means arrived at, for the small leaflets fill the spaces between the larger ones. Configurations similar to this are observable amongst the lower plants also.

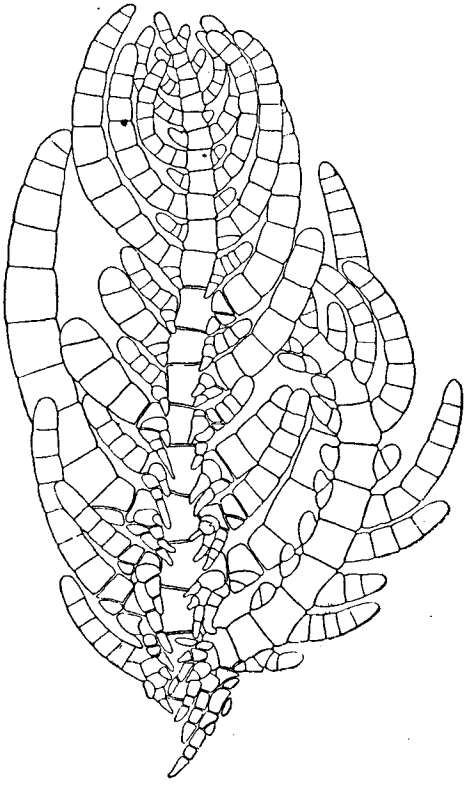

FIG. 80. Euptilota Harveyi. The short shoots are arranged in a pinnate manner on the long shoots; in successive pairs it is alternately the right and left shoot which lags behind in growth. After Cramer.

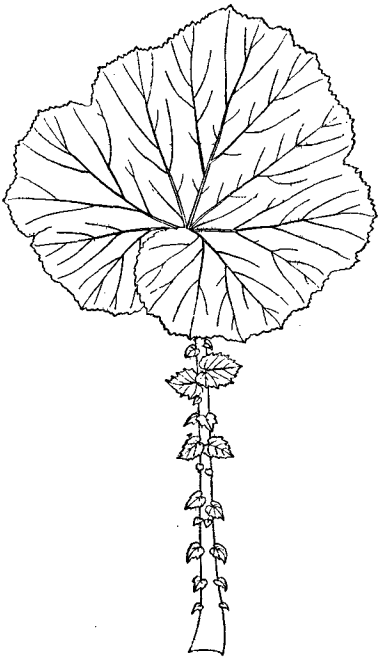

FIG. 81. Geum bulgaricum. Leaf. The terminal lobe very greatly enlarged, the lateral pinnules of unequal size, mostly in alternating smaller and larger pairs. Reduced.

Fig. 80 is a representation of an alga which exhibits an 'interruptedly pinnate' long shoot, inasmuch as alternately on the right and on the left a shoot lags behind in the development. The details of the configuration are probably regulated by correlation between the several parts concerned—the enlargement of some causing others to remain small; in the leaves of higher plants at least there appears to be no definite rule as to which leaflet remains small, although in some cases position determines this. The leaflets which are turned to the axis in

the horse-chestnut, the lupin, and many other plants, remain smaller than those turned away from it, and thus the leaf-surface is carried more to the outside; the smaller leaflets are in these cases the last laid down.

Geum bulgaricum supplies an interesting case (Fig. 81). Here the leaf looks as if it were changing from an interruptedly pinnate one to a simple one. The terminal leaflet is very large, and its position gives it the appearance of a peltate leaf. The lateral leaflets are almost covered by it and are correspondingly reduced; their differences in size can however be always recognized. In other species of Geum the difference between the lateral leaflets and the terminal one is not so great.

V

RELATIONSHIPS OF SYMMETRY OF FLOWERS AND INFLORESCENCES.

FLOWERS.

I have already pointed out that both radial and dorsiventral construction is found in flowers. Flowers which are divisible by two or more planes of symmetry and flowers in which this is not the case occur, apparently without rule, upon plants with radial flowers. The former are only possible if the flowers be cyclic, the latter when they are acyclic, but this difference is of no moment in a general consideration of the condition. The expressions 'regular' and 'irregular' are perhaps best avoided. In most dorsiventral flowers the plane of symmetry passes through the median of the bract[1]; seldomer it is transverse to this, as in Corydalis and in Fumaria (in which one of the two transverse petals is spurred), Wachendorffia thyrsiflora[2], and others. The flowers of Fumaria and Corydalis are twisted subsequently through an angle of about 90°, so that the spur which was originally lateral comes to lie in the median plane. An oblique position of the plane of symmetry is not infrequent in flowers which stand in cymose inflorescences, for example in Commelinaceae, Aesculus, and others; it is not however the cymose character of the inflorescence, but the position of the flowers to one another which is critical here. Thus if we examine the diagram of an inflorescence of Commelina coelestis (Fig. 82) we observe that the several flowers are all indeed obliquely dorsiventral, but through this

[1] The so-called 'median-zygomorphy.'

[2] See Eichler, in Sitzungsber. der Gesellsch. naturforsch. Freunde zu Berlin, 1880.

position the side of the flower upon which the sterile stamens stand is turned *towards the outer side* of the zigzag inflorescence. There can be no doubt that this arrangement stands in direct relation with the pollination. The relationships of symmetry of the *several flowers to one another* and the subordination of the symmetry of the individual flower to that of the whole inflorescence, even in completely asymmetric flowers, are matters requiring consideration, although up till now they have not attracted attention. In Calathea the flowers are in pairs, each flower is so constructed that it cannot be divided by one plane symmetrically, but the two flowers together form a symmetric whole[1]. The flowers of Valeriana are also quite asymmetric.

With reference now to dorsiventral flowers, we have to distinguish two cases: either (1) the flowers are laid down radially and become dorsiventral in the course of their further development; or (2) they are dorsiventral from the beginning—the dorsiventrality appearing at the vegetative point of the flower when its parts are laid down[2], as happens in Reseda and Leguminosae.

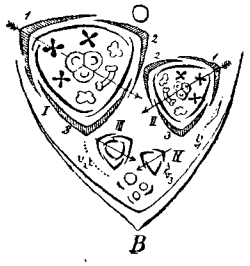

FIG. 82. Commelina coelestis. Diagram of an inflorescence. The arrows indicate the plane of symmetry of the several flowers; these all turn the same side outwards, that, namely, on which the sterile stamens, indicated here by crosses, stand. After Eichler.

1. Most dorsiventral flowers are laid down as radial structures and only subsequently become dorsiventral. The period at which the change to dorsiventrality takes place varies, the earliest is observed in cases where during the unfolding of the flower-bud the position of the flower-parts is so altered that a dorsiventral construction appears, and the change is the result of external influences[3]. In Epilobium angustifolium and Epiphyllum truncatum, for example, it is produced by the reaction to gravity, and according to Focke the curvature which the style of Lilium auratum and of L. lancifolium exhibits is a heliotropic phenomenon. The consideration of the details of these movements belongs more to experimental physiology, here I will only point out that to the category of which I speak belong probably those plants in which radial and dorsiventral flowers both occur in one and the same individual, or in different individuals of the same species. According to H. Müller[4], Saxifraga stellaris, which has usually radial erect flowers, produces

[1] Hofmeister has, as in so many other cases, not overlooked this; see Allgem. Morph. p. 581, With regard to the Zingiberaceae see F. Müller, Schiefe Symmetrie bei Zingiberaceenblumen, in Ber. der deutsch. bot. Ges. v. p. 99.

[2] For details see the account of the development of the flower in Part II of this book.

[3] Dufour, De l'influence de la gravitation sur les mouvements de quelques organes floraux, in Arch. d. scienc. phys. et nat., période 3, xiv. p. 413; Vöchting, Über Zygomorphie und deren Ursachen, in Pringsh. Jahrb. xvii.

[4] H. Müller, Alpenblumen, p. 535.

upon the same stock flowers turned to the side and in part dorsiventral which have smaller upper petals with smaller yellow spots. It is possible to find in Soldanella pusilla stocks with vertically pendent flowers which are radial, and others with flowers inclined obliquely downwards, the corollas of which are somewhat more expanded on the under side[1]. It is of special interest to observe in the cases that have been quoted that the dorsiventrality is induced by external factors, and that these only operate at a late period after the opening of the flower.

2. In the second category of flowers the dorsiventrality is brought about before the unfolding, and here, as Noll[2] was the first to show, we must distinguish two groups of dorsiventral flowers according to their physiological relationships :—

(*a*) Those which Noll has termed 'essentially zygomorphous,' characterized by the fact that their disposition is always of a definite kind. In its 'normal position' the dorsal side of the flower is turned upwards, its ventral side downwards, and the entrance is always directed away from the axis of inflorescence. The flower is thus most favourably placed for the visit of insects, and if it be displaced it always recovers its normal position by definite movements. Such flowers react then to changes of position differently from radial flowers.

(*b*) The 'unessentially zygomorphous' flowers of Noll are, on the other hand, those which stand on the margin of the inflorescences of Iberis and others amongst the Cruciferae, of Heracleum, Coriandrum and others amongst Umbelliferae, of Compositae, Dipsaceae, &c. They become in a morphological sense dorsiventral, because the outwardly directed portion of the corolla is more strongly developed than is the inner. These flowers react to changes of position in the same way as do their sister-flowers which are radial, they merely serve to increase the attractive apparatus for the whole inflorescence, and the dorsiventrality of the corolla stands in no direct relationship to the pollination of the several flowers. That this is so is shown by the fact that in many flowers the same result is arrived at although the dorsiventrality does not reach the corolla, the androecium and the gynaeceum. This happens in some Rubiaceae. Some years ago, during an excursion in the Ghats Mountains in India, I met with shrubs on whose bright flower-clusters when at considerable distance I thought I saw white butterflies. The shrubs were species of Mussaenda, about the flowers of which I made at the time the following note :—'On certain of the *outer* flowers of the inflorescence one sepal is greatly enlarged, and has become leaf-like,

[1] Herbert Spencer, Principles of Biology, ii. p. 153, figures a similar case in Campanula.

[2] Noll, Über die normale Stellung zygomorpher Blüten und ihre Orientierungsbewegungen zur Erreichung derselben, in Arbeiten d. bot. Instituts in Würzburg, iii.

only it is quite chlorotic, and has no trace of chlorophyll. These white leaves make the inflorescence conspicuous from afar. The inner flowers have five linear small sepals.' Pogonopus Ottonis, another rubiaceous plant, which I met with subsequently in Venezuela, exhibits similar features. In these Rubiaceae then only one sepal in the peripheral flowers is differently constructed, the flowers remain otherwise radial. When one endeavours to give a causal explanation of the occurrence of dorsiventrality in flowers these cases must evidently be distinguished from the others. In most of the examples of this kind the flowers are laid down as radial structures, but by the preference given to the outer part of the perianth they become dorsiventral. In the 'essentially' dorsiventral flowers also the dorsiventrality comes about either through the different construction of the parts of the flower which are laid down radially, or through the inner parts of the flower being laid down in different number or with a different construction from the outer; often enough both processes are combined, but then usually in such a way that a dorsiventral flower results, or, in other words, the relationships of symmetry of the several whorls of the flowers do not change independently one of the other. Every systematic work supplies examples of this, and especially Eichler's 'Blütendiagramme.' I need only refer to Fig. 82, copied from Eichler, which shows how a flower laid down radially may by differences in construction of the androecium become dorsiventral. The flowers of Commelina, like those of most monocotyledonous plants, consist of five trimerous whorls, a radial arrangement which permits of symmetric division in three different planes; but of the six typical stamens only three are completely formed, the other three, indicated in the diagram by crosses, are sterile, and diverge also in the form of their cruciform four-lobed anthers from the three fertile ones. The flower has therefore become dorsiventral and can only be divided symmetrically in one plane, and associated with this we observe that the fertile stamen through which the plane of symmetry falls differs in construction from the other two by its possession of a broader connective. The same change of symmetry would have been brought about if the three outer stamens had been suppressed, as often happens. It is however by reduction in the number of the carpels that the whole symmetry of the flower is chiefly influenced, as will be pointed out more particularly when the morphology of the flower is discussed, at the same time most striking expressions of change of relationships of symmetry are observed in the construction of the flower-envelope, especially the corolla, in proof of which I need only refer to the 'labiate,' 'ligulate,' 'personate,' and 'calcarate' flowers.

The relationships which I have just briefly sketched have from an early period begotten explanations which have been partly teleological,

partly causal. Christian Konrad Sprengel [1] was the first who endeavoured to establish the teleological explanation which at the present time, although with a somewhat different meaning, is regarded with most favour. 'As in so many other things, there are three circumstances out of which one can find an explanation of the structure of flowers, and of why they are regular [2] or irregular [3]. The first is the inflorescence, that is to say, the method in which the flowers are arranged on the stem or the branches of a plant. The second is, that the raindrops, at least when the air is calm, fall perpendicularly upon the flowers. The third is the intention of nature that the flowers should be fertilized by insects, in connexion with which it must be remembered that the insects, whether flying or moving otherwise, generally maintain an erect position.' 'Neither from the side of the insect nor from that of the rain is there the slightest reason why . . . a flower which is strictly erect, or strictly pendant . . . should not be regular . . . the insect wherever it alights upon it can fertilize it; on the other hand horizontal flowers because they have an upper and an under side [4], and the insect usually alights upon the under side, and creeps in upon one of the two . . . must be irregular.'

By the principle of selection the appearance of dorsiventrality in flowers finds its 'explanation' in the advantages which spring from it. 'The zygomorphous structure of the flower allures agents for crossing and excludes useless robbers of the honey. More seeds are produced by crossing, and the plants produced from them are more resistent and more vigorous than those which are the result of self-fertilization. The better the flower-structure is adapted to agents of crossing the stronger will be the progeny which will hand on the peculiarities of the best-fitted individuals to descendants [5].' If however these forms of flowers were produced entirely by variation in any direction and by survival of the fittest, it is difficult to see why many terminal flowers should not also have become dorsiventral; besides there are also anemophilous plants, whose flowers, as those of many grasses, are dorsiventral [6]. In my opinion we have in the position of the flower an element of special importance, and the behaviour of the flower in becoming dorsiventral only after unfolding must

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[1] Sprengel, Das entdeckte Geheimnis der Natur, &c., Berlin, 1793, p. 37. See also Delpino, Zigomorfia florale e sue cause, in Malpighia, i. p. 245; Robertson, Zygomorphy and its causes, in Bot. Gazette, 1888.

[2] Regular = radial.

[3] Irregular = dorsiventral.

[4] Sprengel, l. c. p. 42, has accurately indicated in this the essential character of a dorsiventral flower—the possession of an upper and an under side; the modern expression 'zygomorphous' is based upon a subordinate feature—the existence of a right and left side.

[5] Focke.

[6] The two lower lodicules are alone developed, the upper being useless has aborted and the flower is undoubtedly dorsiventral. Darwin's statement in Forms of Flowers, p. 147, that dorsiventral flowers are unknown in anemophilous plants requires modification.

be taken as a starting-point in any inquiry into this matter. Lateral flowers are in a different position with regard to external forces from terminal flowers. According to the sensitiveness of the former to external factors the configuration of the flower will be changed more or less early. Such changes may become inherited, and flowers so changed will be of course favoured over others, and many of their parts will be aborted as useless members after the introduction of dorsiventral structure. Lateral flowers may however remain radial, as we see in many Malvaceae.

The purely mechanical explanation which was first propounded by A. P. de Candolle[1] must in my opinion be entirely rejected. According to him the position of the flowers has a great influence upon their relationships of symmetry. Every flower which in nature is terminal, erect, and solitary, is radial even if it belongs to a family with usually dorsiventral flowers, as for example, in Asarum amongst the Aristolochiaceae; but if lateral flowers arise below a terminal flower, these will be subjected to the pressure of their neighbours[2], and will grow outwards, where the pressure is less. Other factors, such as inequalities of nutrition, of air, and of light, may also have an effect. When a terminal flower appears in plants which normally have no terminal flower but only strongly dorsiventral lateral flowers, as occasionally happens in some Labiatae, such terminal flowers are radial[3]. He also points to the fact that in the changing of the symmetry of the flower relationships of correlation between the several parts of the flower may also come into consideration.

Hofmeister[4] assumed a causal relationship to gravity in the dorsiventral flowers, just as he did in the dorsiventral shoots.

Lastly we have the recognition by Darwin of 'the supreme dominating power of insects on the structure of flowers'[5]; and then the view that the stimulus which the insect exercises may influence the form of the flower[6], which is thus expressed by Henslow[7]: 'I regard this cause as issuing from the insect itself; namely the mechanical influence of its weight and pressures.' How this can explain the fact that in orchids and other plants, and in the dorsiventral marginal flowers above mentioned, the right disposition of the flower only comes about in the unfolding I am unable to see; the whole idea is a subjective conjecture without any practical proof whatever.

We have indeed in the fundamentals of this question not reached

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[1] De Candolle, Théorie élémentaire de Botanique. Paris 1819.

[2] Neither here nor in other cases where this 'pressure' is assumed as an agent modifying form is any proof furnished of its existence.

[3] Such 'peloria' occur also in other plants; see Section IV of this book.

[4] Hofmeister, Allgemeine Morphologie, p. 581. [5] Darwin, Forms of Flowers, p. 147.

[6] See Naegeli, Mech.-physiol. Theorie der Abstammungslehre, where the influence of the scrambling of the insects upon the form of the corolla, &c. is fantastically described.

[7] Henslow, Floral Structures, p. 103.

much further than the point of view established by Sprengel and de Candolle. We know that dorsiventral construction of the flowers in most cases is connected with pollination and only occurs in lateral flowers.

INFLORESCENCES [1].

We have here, as in the case of the flowers, two cases to look at, namely:—inflorescences which are laid down as radial structures, and only become dorsiventral by torsion of the flower-stalks or of the internodes of the axis of inflorescence; and inflorescences in which the dorsiventrality exists from the beginning. Flowers on dorsiventral inflorescences are usually only shortly-stalked, and to the inflorescence is assigned the task of bringing them into the correct position for pollination. With regard to biological relationships we have to distinguish two cases—dorsiventral inflorescences are found in both anemophilous and entomophilous plants.

1. Anemophilous plants.—In the inflorescences of Urtica dioica Dorstenia, some Gramineae, and others, the flowers all stand upon the upper side. In Urtica dioica the branches of the inflorescence also have this position. We may perhaps find the biological significance of this in Urtica dioica in connexion with the fact that the anthers explode, for the pollen discharged as a small dust-cloud will have a better chance of being transported by currents of air when sent upwards, than it would have were it shot out in other directions. Urtica urens is monoecious and its inflorescences are not dorsiventral.

Dorsiventral inflorescences of a striking kind in which the spikelets are inserted unilaterally on the whole inflorescence are found in many grasses, for example, Chloris, Dactylis, and others. It is scarcely possible to see a relationship to the environment in these; but if we examine from the comparative biological standpoint the arrangements of the inflorescence of grasses, it is evident that the configuration of the inflorescence is so moulded that it can be easily moved by the wind. The slender haulm, the spikelets, which in the quaking grass are seated upon long thin stalks, the delicate spreading branches in others, all serve the same end, which is also followed up in the configuration of the stamens, namely, to secure the easy scattering of the pollen. Now unilateral inflorescences occur, as far as I know, only in grasses which have shortly-stalked spikelets, and where they are displaced to one side, as in Dactylis, they offer a larger surface to the wind than they would do were they distributed equally all round the axis. But even in the cases where the small number of spikelets prevents us looking at them from this point of view, the

[1] See Goebel, Über die Verzweigung dorsiventraler Sprosse, in Arb. d. bot. Inst. in Würzburg, ii (1880).

unilateral branching promotes a more frequent oscillation to and fro than would otherwise be the case. Remembering the existence of grasses with radial inflorescences we see in how great a number of ways the same end can be arrived at in one and the same family.

2. Entomophilous plants.—In plants which occupy a position in which they are subjected to a unilateral strong illumination, as for example on the edge of woods, and in inflorescences which grow on thick bushy plants, the attractive apparatus of the flowers is more effective when it is only turned to the one, that is the illuminated, side. I have elsewhere pointed this out[1] and Urban[2] has further elaborated the point. The most striking illustrations of this are to be found in cases where the dorsiventrality of the inflorescence is determined in the primordia, and of this I shall give an example. Fig. 83 represents a transverse section through the bud of a flowering plant of Vicia Cracca. It has

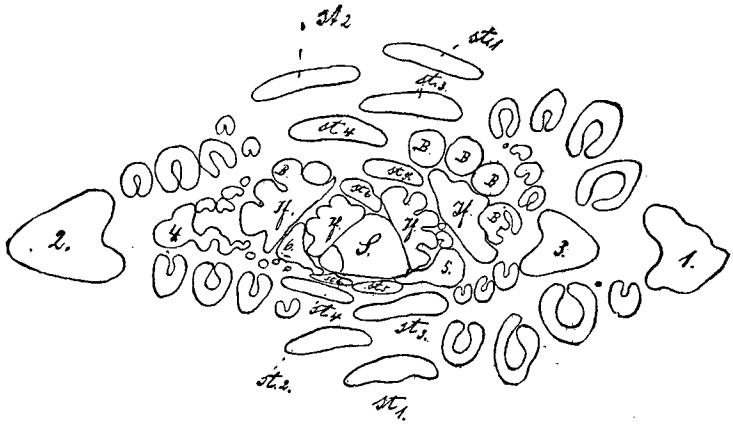

FIG. 83. Vicia Cracca. Transverse section through the end of a flowering shoot. *S* shoot-axis. Four inflorescences and six leaves are represented; an inflorescence, *If*, arises in the axil of each of the leaves 3, 4, 5, and 6; inflorescences do not however stand before the middle of their bracts but are towards the side of the chief axis which is directed upwards. *B* the flowers of the older inflorescences; all the flowers stand upon the side turned away from the chief axis. The pinnules of the older leaves are recognized by their involution; st_1–st_6 stipules of which those upon the upper side are larger than those upon the under side. See also explanation of Fig. 78.

two rows of leaves and the section has been made through leaves numbered 1 to 6. The inflorescences, *If*, stand in the leaf-axils but they are all turned to one side (in the figure directed upwards), because each is not exactly in the median of the axillant leaf, but appears as displaced towards a stipule[3]. In the leaf-axil upon the side turned away from the inflorescence there appears later a vegetative shoot (see Fig. 79, page 126). In each inflorescence the flowers are arranged upon the side turned away

[1] Goebel, Über die Verzweigung dorsiventraler Sprosse, in Arb. d. bot. Inst. in Würzburg, ii (1880), p. 399.

[2] Urban, Zur Biologie der einseitswendigen Blütenstaude, in Ber. der deutsch. bot. Ges. 1885.

[3] This is a primary position, not the result of a displacement.

from the chief axis, *S*, and this is due to the fact that at an early period before the appearance of the flowers the axis of inflorescence is flattened upon the other side which lies closely adpressed to the chief axis. This side bearing no flowers then becomes strongly convex, by which a good protection is provided for the young flower-buds. Subsequently the axis of the inflorescence straightens in a negative geotropic direction, and is orthotropous in spite of its dorsiventrality. Comparison with other Leguminosae shows that this dorsiventral inflorescence is probably derived from a radial one.

Speaking of this leads me to mention the dorsiventral circinate inflorescences which are found in many, although not all, Borageineae and Hydrophylleae, in Hyoscyamus, and other plants; such inflorescences are phylogenetically derived from scorpioid cymes [1]. The chief consideration for us here is that they are markedly dorsiventral, bearing flowers upon the upper side and the bracts, where these exist, upon the flanks. The axes of inflorescence are usually obliquely ascending and unfold themselves in such a way that an opening flower always stands upon the highest point of the axis; this flower is thus not only most visible but is also best illuminated, and it is in the highest degree probable that light plays not merely an indirect but a direct part in pollination. It is for example a common belief of gardeners that artificial pollination is more likely to succeed in sunshine than in dull weather [2].

I must refer to my previous publications for further details regarding inflorescences which are dorsiventral from the outset, and I now pass to those inflorescences which are *unilateral* through torsion of their flower-stalks or their axes of inflorescence whilst they were laid down as radial structures. We find such forms amongst the Leguminosae, for example in Hedysarum sibiricum, and others, but also in other families especially in Labiatae, for example in Horminum pyrenaicum, Scutellaria peregrina, and others, in Scrophularineae, for example in Digitalis purpurea and especially Melampyrum, in Pyrolaceae, and also in many monocotyledonous plants, such as Gladiolus, and Freesia. This unilaterality of the inflorescence is specially striking when the bracts originally standing in decussate pairs are brought through torsion of the axis of inflorescence to lie in two rows which converge in many cases to that side of the inflorescence which bears no flowers, whilst the flowers themselves bend

[1] For the literature of this subject see Goebel, Über die Verzweigung dorsiventraler Sprosse, in Arb. d. bot. Inst. in Würzburg, ii (1880). Where, as in Borago officinalis, the flowers have long stalks and large corollas the inflorescence is as good as not dorsiventral, and is really a true scorpioid cyme as it occurs in Scrophularia.

[2] This may be a consequence of the secretion from the stigma, and we must remember the amount of transpiration is different in the sun from what it is in diffuse light. The matter deserves careful investigation.

towards the other side, as happens in Melampyrum pratense and M. sylvaticum, Scutellaria peregrina; in this way the flowers at flowering time may no longer be enveloped by the bracts.

I have no doubt that the unilaterality of the inflorescences just mentioned is in many cases caused by external factors, and one is disposed to agree with Vaucher[1] that light has a predominating influence. He says for example regarding Melampyrum: 'This direction of the flowers to the illuminated side is so marked that Melampyrum sylvaticum, which only grows in the middle of a wood, enables one to determine which side of the wood receives most light. I have often noticed the flowers of one plant directed differently according to their elevation on the plant. . . .' Noll's investigations[2] however show that the influence of light is not conspicuous everywhere. At the edge of a wood the inflorescences of Digitalis all turn the side bearing flowers towards the light, but even if the plant be illuminated on all sides the inflorescences are still sharply unilateral. The axes of inflorescence show from a certain age onwards a curvature of nutation and therefore become overhanging, the flower-stalks are positively geotropic, the flowers must therefore be turned to one side and are, on lateral inflorescences, necessarily turned away from the chief axis. In unilateral illumination the axes of inflorescence curve in a positively heliotropic manner. The same is probably the case in Convallaria Polygonatum and others, and in the conspicuous unilateral inflorescences of species of Scutellaria[3]. In this latter species the flowers on plants which are strongly illuminated from one side are all turned outwards, and a torsion of the internodes of the inflorescence takes place alternately in an opposite direction whereby the bracts of the flowers which originally stood in cross-pairs come to lie almost in two rows. The axes of inflorescence also hang over through 'spontaneous nutation,' and the direction of the overhanging determines that of the unilaterality as in the case of Digitalis, but the flower-stalks are positively geotropic. As the plagiotropous lateral shoots springing from the axils of the leaves of the chief shoots bend away from the chief axis, the flowers must all be turned to the outside. The total result here then will depend upon the following factors:—

1. The assumption of an inclined position on the chief axis, which I would designate simply as plagiotropous.

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[1] Vaucher, Histoire physiol. des plantes d'Europe, vol. iii, p. 543. See also Wiesner, Die heliotrop. Erscheinungen im Pflanzenreich, p. 62.

[2] Noll, Über die normale Stellung zygomorpher Blüten und ihre Orientierungsbewegungen zur Erreichung derselben, in Arbeiten d. bot. Instituts in Würzburg, iii, p. 235.

[3] See regarding this Noll l. c. and Kolderup Rosenvinge, L' Organisation polaire et dorsiventrale des plantes, in Revue générale de Botanique, i.

2. The oblique direction of the lateral axes is influenced by the chief axis. They all curve away from the chief axis.
3. Internodal torsion of the axis of inflorescence as in other plagiotropous shoots.
4. Positive geotropism of the flower-stalk.

We see in the dorsiventral inflorescences that nature seizes, so to speak, the good where it finds it; how this originates is a matter of no importance. In definite circumstances it is of advantage that the flowers be directed towards one side, and this may be brought about partly by curvatures—heliotropic, geotropic, plagiotropic position of the axis of inflorescence—partly by laying down of the flowers upon one side; and that unilateral illumination may bring about an internodal torsion which results in decussating leaves taking a two-rowed position, I have already shown in Urtica dioica [1].

In what I have said it has been assumed as probable that the dorsiventral inflorescences have proceeded from radial ones. We see too that in the inflorescences which are *unilateral* this process does take place in the course of the development. We do not know the cause or causes (because the ways may have been different) which have conditioned the origin of the inflorescences which are from the first laid down as dorsiventral. In the Leguminosae the absence of the flowers upon one side of the inflorescence has been explained [2] by the assumption that their development has been hindered by the pressure of the chief axis against which the inflorescence lies closely adpressed on one side (see Fig. 83), and in Trifolium rubens and Medicago sativa, which have only a portion of the base of the inflorescence wanting flowers, a similar explanation has been given. But it is quite possible that the causal relation may have been the converse—that no flowers having arisen their room was used in a better way and that thus the adpression occurred. It can be nowhere proved that such coarse mechanical relationships as those of pressure exercise so far-reaching an influence upon the configuration. Amongst the Leguminosae, too, there are species of Trifolium in which the laying down of the flowers is at first unilateral and then gradually the whole inflorescence is laid claim to without any relationships of pressure whatever having come into operation. The peculiarity of the inflorescence is much more probably here fixed from the beginning in the form of its vegetative point; the absence of the flowers upon the one side may rather stand in connexion with the fact that their function having become enfeebled, abortion was their fate. Still, as I have said, the way in which this has been brought about has yet to be discovered.

[1] Goebel, in Botan. Zeitung, 1880, p. 843.

[2] First of all by Godron, Observations sur les bourgeons et sur l'inflorescence des Papilionacées. Nancy, 1865

THIRD SECTION

DIFFERENCES IN THE FORMATION OF ORGANS AT DIFFERENT DEVELOPMENTAL STAGES. JUVENILE FORMS

BOMBAY BRANCH OF THE ROYAL ASIATIC SOCIETY

DIFFERENCES IN THE FORMATION OF ORGANS AT DIFFERENT DEVELOPMENTAL STAGES. JUVENILE FORMS[1]

INTRODUCTION.

ALL living beings are, as is well known, in a condition of continual change unless they are in that state known as 'latent life,' and we have in this section to consider the outward changes of configuration which are associated with this changing condition. As a rule these are more manifold the higher the organization exhibited by a plant. In lower plants in which a separation of generative from vegetative plasm has not yet appeared, Bacteria and Conjugatae for example, the changes of form in the course of development are very simple, but in the more highly differentiated plants there is bound up with the formation of the sexual propagative organs a climax of development which corresponds in a certain degree with the 'climacteric' of animals, in that the vegetative parts die off sooner or later, although in some trees which are not exhausted by the formation of seeds the numerous vegetative points may theoretically be regarded as having unlimited existence. In these cases it has rightly been considered that external unfavourable conditions are responsible for the fact that a gradual cessation of vegetation takes

[1] At p. 251 of my 'Vergleichende Entwicklungsgeschichte der Pflanzenorgane' I have given an account of the subject treated of in this chapter, and further information will be found in my papers 'Über die Jugendzustände der Pflanzen' in Flora, 1889, p. 1, and 'Über Jugendformen von Pflanzen und deren künstliche Wiederhervorrufung' in Sitzungsberichte der kgl. bayer. Akademie der Wissenschaften, math.-naturw. Classe, 1896. The literature, so far as it relates to Spermaphyta, is collected by C. Schäffer in his treatise 'Über die Verwendbarkeit des Laubblattes der heute lebenden Pflanzen zu phylogenetischen Untersuchungen,' in Abhandl. aus dem Gebiete der Naturwissenschaften, herausgegeben vom naturwissenschaftlichen Verein, Hamburg, Bd. xiii (1895).

place, which is indicated by shortening of the shoot-axis and other signs, and that finally death ensues; the relationships are here complicated by the concatenation of numerous generations of shoots. In other cases however *internal* causes are certainly operative in limiting the development, and of these the relationships of correlation between the generative and the vegetative cells are probably the most effective.

Of this nature is the case of the prothallus of Selaginella. The macrospore can take only water from the outside; the development of the prothallus is therefore limited because it does not produce chlorophyll. The food-material it contains is utilized for the formation of a number of archegonia which arise apparently independently of light as the material necessary for their construction was derived from the sporiferous plant. But the growth of the prothallus of Salvinia is also limited, and yet it possesses chlorophyll and continues to grow if the first-formed archegonia are not fertilized. The material formed by its assimilation is probably however always devoted to the formation of archegonia and it therefore cannot exhibit a strong vegetative growth; the prothallus therefore ultimately dies. The prothalli in the Marsiliaceae also show a continued vegetative growth if the archegonia remain unfertilized although this is limited in point of time. The energy which exists in the prothallus is exhausted by the formation of the archegonium which is its chief duty, and new energy cannot be again added to it. In the higher plants also in certain circumstances the material contained in the seeds may be utilized for the production of flowers and fruits; at least seedling plants placed in sterile soil with access to light may form a few seeds, but this is only the case in plants which have a rich store of reserve-material. Analogous cases are known also in lower plants. Under unfavourable conditions the development of a germ-cell may be entirely limited to the production of another germ-cell; for example, the spores shed from Empusa Muscae if they do not reach a fly produce a short germ-tube almost the whole protoplasmic content of which is devoted to the formation of a new spore. The spores of Cladosporium form a sporophore, or even directly new spores, instead of a mycelium, if they be cultivated in conditions which exclude as completely as possible all nutritive material but allow access of light and sufficient moisture[1]. The spores of Mucor racemosus if they germinate in distilled water form a feeble mycelium upon which a small sporophore may arise, and Klebs observed[2], in experiments carried on in rarefied air, that an individual spore lying in the sporangium was developed into a small but normal sporophore. The cells of the gemmae of Lejeunia Metzgeriopsis, which normally grow out into a

[1] Schostakowitsch, in Flora, lxxxi (1895), p. 370.

[2] Klebs, Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen, p. 496.

thallus of considerable circumscription, may give rise to new gemmae[1]. Obviously the plant here saves the 'germ-plasm' by the shortest possible way under conditions which are unfavourable for development. But commonly there is intercalated between germination and the formation of the germ a long series of developmental stages which are of advantage to the species because they make possible a considerable increase of the plant-body and through it the formation of *numerous* germ-cells.

The appearance of these germ-cells always marks a climax of development, in many cases its conclusion, which is only gradually reached. The first stages may be called the *juvenile stages.* It is of course impossible to limit these sharply[2]. The difference between these juvenile stages and the *adult form* may be more or less great. These two stages naturally include again series of developmental processes which pass one into the other without distinct limitation. The difference between the two is expressed not only in configuration, but frequently also in other characters particularly in the capacity for reproduction. The first leaves of the germ-plant of Lycopodium inundatum, for example, possess the capacity of producing adventitious shoots, but this is wanting in those which are formed later[3]; in Utricularia montana we find analogous phenomena; and in many Coniferae cuttings of the juvenile form root readily, whilst those of the adult form do so with difficulty or not at all[4]. The juvenile form also exhibits different relationships of direction: in many plants, for example, Tilia, Fagus, Carpinus[5], whilst the seedling is orthotropous the later shoots are plagiotropous; in other plants, for example, in the Marcgravieae and in the root-climbers amongst the Aroideae which will be referred to later, the opposite relationship is observed. This is only one of the numerous examples showing that *the adaptation of the juvenile form to external relationships is different from that of the adult form,* a fact which appears in a very striking way in the 'larval form' of many animals. The differences between the two sections of the developmental history show themselves in very different degrees; there are cases where they are very slight and the two sections may quite gradually pass one into the other. I have designated this latter condition the *homoblastic* development, and that in which the differences are great the *heteroblastic.*

Amongst higher plants Casuarina may serve as an example of the

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[1] Goebel, Morphologische und biologische Studien, in Annales du jardin botanique de Buitenzorg, vii. p. 71.

[2] We are here concerned only with the features which appear after germination and not with the arrangement of the cells and the configuration of parts which obtain, for instance, in the embryo within the seed of one of the higher plants.

[3] See what is said below about Preissia commutata.

[4] See page 51.

[5] See page 70.

homoblastic development (Fig. 84). The shoot-axes of this plant contain chlorophyll and, like those of Equisetum, have rudimentary cyclic leaves concrescent in a sheath. This character appears in the seedling above the cotyledons. The whorl following the cotyledons is two-membered and the leaves are at right angles to the cotyledons; thereupon follows a second decussating two-membered whorl; the third is four-membered, and the members cross those of the second diagonally [1]. The horse-tail itself presents the same features:—The axis of the germ-plant is much slenderer and has a simpler anatomy than the axis of the later shoots; the number of leaves in a whorl is smaller; subterranean shoots are wanting; and it forms shoot-generations which are successively stronger until the definite adult form is reached, but the outline of the configuration is the same in all shoots.

FIG. 84. Seedling plant of Casuarina torulosa. Magnified 2.

Heteroblastic development is exhibited by the Australian species of Acacia which possess phyllodes, and is also seen elsewhere especially in Bryophyta and many Algae. Examples of this have specially attracted attention when, as happens in the case of Acacia, the configuration of the seedling resembles that of the adult form in allied plants. Many species of Acacia have permanently the leaf-form which appears only at germination in those producing phyllodes, and the configuration of the seedling places directly before our eyes the transformation which has taken place. The retention by the seedling in this case of the original, phylogenetically older, form of the vegetative organs is connected with [2] its living under other conditions than does the adult form. But in other cases the configuration of the seedling certainly does not turn upon the retention of an original relationship of form, but is an adaptation [3] developed later, and the seedling exhibits then derived, not primitive, characters. The adaptation to other relationships does not of itself furnish us with any explanation of the character; this is obtainable only by comparison with allied forms. In many cases too the distinction we have just pointed out cannot be drawn with any certainty; within one and the same cycle of affinity, and even within one and the same genus, the configuration of the juvenile form is not always similar.

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[1] See Morini, Contributo all' anatomia del caule e della foglia delle Casuarinee, in Mem. della R. Accad. delle scienze dell' istituto di Bologna, ser. v. T. iv. p. 692.

[2] See below on p. 153, and following pages.

[3] Such are the different contrivances for nutrition of the embryo and for facilitating germination, about which, so far as they have morphological interest, some account will be given in Part II of this book.

In addition to the varying behaviour of the juvenile form towards the external conditions of plant-life, there is another factor to be considered which finds special expression in the configuration of the leaves of the juvenile stage. The difference in the configuration of the juvenile leaves compared with that of the adult ones is frequently due to the fact that they are *arrested formations;* in other words, the development of the leaves is the same in both juvenile and adult, but in the juvenile the primordium of the leaf is arrested in its development at a certain stage and therefore the leaf exhibits an evident, often extremely, different configuration. This point in the history of development must also be applied to the explanation of the differences between the configuration of those juvenile forms which have been already referred to as phylogenetically primitive and the adult forms, inasmuch as the latter have acquired their different character by passing through a further transformation.

In many plants *reversion* of the adult to the juvenile form frequently occurs. This will be specially dealt with in subsequent pages.

What follows does not profess to be a comprehensive and systematic account of the development of the different plant-forms, but in accordance with the aim of general organography an attempt has been made to select from the different groups of plants examples which shall exhibit the characteristic configuration of the juvenile form, and to place them before the reader in such a way as shall best bring into prominence the different sides of the problem. The configuration of the cotyledons in the Spermaphyta is therefore entirely passed over here, that will be spoken of in the special part of this book; I need only say here that the cotyledons which so frequently differ in form from the foliage-leaves are merely arrested forms of these, the arrest being sometimes permanent, sometimes transient. The cotyledons of Ampelopsis furnish examples of the latter; they are originally small and simple, but after germination they grow into relatively large *foliage-leaves.* Even more striking are the phenomena observed in many species of Oenothera [1], where, by intercalary growth at the base of each cotyledon after germination, a portion is interposed which is much larger than the original cotyledon. In these plants then the arrest in the development of the cotyledons lasted only during the period of rest in the seed and the first stages of germination, and the difference between this and what happens in most other cotyledons is, in my opinion, only quantitative, not qualitative.

The *duration* of the juvenile form is scarcely less variable than its external configuration, and is frequently dependent upon external factors, especially in lower plants. In some of these the juvenile form is the

[1] See Lubbock, A contribution to our knowledge of seedlings, i. p. 553. London, 1892.

characteristic vegetative body, the chief duty of the adult form is to produce the sexual organs, and it appears as a short-lived appendage of the juvenile form. In consequence of this the juvenile form may acquire so much of an independent character that it develops special propagative organs, from which of course juvenile forms only are again produced. We shall presently see that in some of the Coniferae the 'juvenile form' may even go the length of forming sexual organs, and we have then before us plants in which a section of the development which elsewhere appears as the 'adult form,' and is of great importance for the specific character, appears to be entirely excluded. As examples of plants in which the

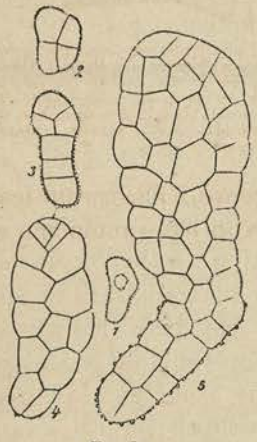

FIG. 85.

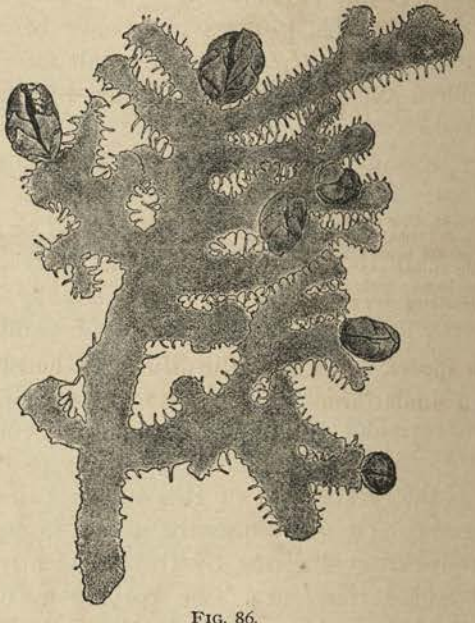

FIG. 86.

FIG. 85. Lejeunia. Germination of the spore. A flat cellular 'pro-embryo' with a two-sided apical cell is produced. When it has reached a limited size the leafy plant develops from its apical cell.

FIG. 86. Lejeunia Metzgeriopsis. The 'pro-embryo' is the special vegetative body, and upon it the leafy shoots appear as small appendages, the only function of which is to support the sexual organs. Not so highly magnified as Fig. 85.

juvenile form has a prolonged existence, whilst in allied forms it is only a developmental stage rapidly passed over, I may note here only two members of the Bryophyta which exhibit the phenomenon in a specially simple manner. Lejeunia Metzgeriopsis (Fig. 86) possesses a richly-branched thallus of a band-like form, which multiplies freely by means of disc-shaped gemmae. This liverwort is nevertheless a foliose one, and the thallus is merely an extended development of the juvenile form which appears in germination of other species of Lejeunia (Fig. 85). The leafy shoots which constitute the characteristic vegetative organs in other members of the genus are only supporters of the sexual organs in Lejeunia

Metzgeriopsis, and the juvenile form continues as the vegetative body of the plant possessing independent propagative organs in the form of gemmae, which are probably more important for the spread of the plant than are

FIG. 87. Ephemerum serratum. Protonema with seven (male and female) plants. The large female plant to the left of the figure—(it overlaps the male ones standing beside it)—has produced a sporogonium which is nearly ripe. In the middle are three leafy plants in a cluster; this is uncommon, they are usually in pairs.

FIG. 88. Ephemerum serratum. Portion of thread of protonema with two young plants. Three antheridia are visible in the plant to the left, and one archegonium in the plant to the right. The first leaf of the female plant is seen turned to the front and consists of one row of cells. More highly magnified than Fig. 87.

the spores. Amongst the Musci we find in the genus Ephemerum features of a similar kind (see Figs. 87 and 88). The thread-like protonema which

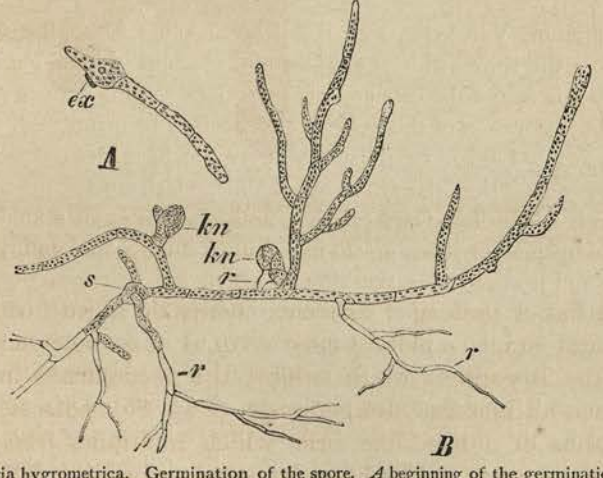

FIG. 89. Funaria hygrometrica. Germination of the spore. *A* beginning of the germination, *ex* exine. *B* protonema with two young moss-buds *kn*, one of which has sent out a 'root' *r*; *s* spore. After Müller-Thurg u. Magnified. Lehrb.

usually appears in the group (Fig. 89) only as a juvenile form persists, and far surpasses in development the leafy shoots, and these are merely bearers of the sexual organs. In both these cases the long duration of the juvenile

form is an inherited character; how far we are justified in regarding it as an original one, or as acquired through adaptation, will be discussed when I speak of the Bryophyta in the second part of this book, and therefore I only briefly refer to the group in this place. I shall subsequently show that external circumstances also have been proved in a number of cases

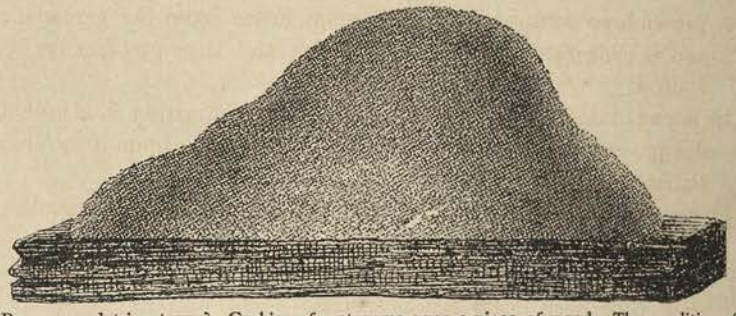

FIG. 90. Bryum pseudotriquetrum? Cushion of protonema upon a piece of wood. The conditions for growth having been most favourable this unusually large development of protonema has taken place, and at the same time the production of moss-buds has been retarded. Natural size.

to retard the appearance of the adult form, and therefore the duration of the juvenile form can be prolonged beyond its usual period (Fig. 90). The peculiar behaviour of many conifers in this respect will be noticed presently.

I now proceed to give some illustrative instances from different groups of the Plant Kingdom:—

1. THALLOPHYTA.

In Oedogonium, Vaucheria, Fucus, and some other Algae, the sexually-mature plants grow from the spores without any essential changes of form, but there are other Algae in which this is not the case and they produce usually a more or less peculiar *pro-embryo*. In illustration of this some Florideae may be mentioned, amongst which two freshwater forms, Lemanea and Batrachospermum, have been carefully investigated.

Lemanea has a pluricellular cylindrical thallus, which must be regarded as built up out of cell-threads which have fused together, and it produces the sexual organs. The spores produced by these organs grow out into a much simpler 'pro-embryo'[1] composed of cell-threads and upon it the sexual shoots, which have a more complex structure, appear. In this plant as in other instances, mosses, for example (alike those with filiform protonema and those with flat pro-embryo as in Sphagnum), the adult form possesses characteristic root-threads the configuration of which conforms with that of the pro-embryo, and from them new plants can shoot out. They spread upon the substratum and fix the thallus to it. Similar pro-embryos may also, as Brand has recently shown[2], be produced by the vegetative cells of the sexual shoots if these live

[1] This was first shown by Thwaites, 'On the early stages of development of Lemanea fluviatilis,' in Proc. of the Linnean Society of London, vol. i (Feb. 15, 1848), p. 360. See also Wartmann, quoted by Goebel in Flora, 1889.

[2] Brand, Fortpflanzung und Regeneration von Lemanea fluviatilis, in Ber. d. deutsch. bot. Ges., xiv. p. 185.

under conditions of dryness. Lemanea then behaves in this respect in the same way as the Musci (Fig. 91).

The 'pro-embryos' of Lemanea have been partly described as forms of the algal genus Chantransia, and the same thing has happened in the case of the genus Batrachospermum[1]. We may shortly summarize what takes place in this latter genus in the following way:—

1. A pro-embryo composed of cell-threads arises from the germinating spore, and it clings at first to the substratum and thus prepares for its fixation upon it.
2. In normal conditions, of which abundant illumination is a prominent one, this pro-embryo usually attains only a small size; upon it the characteristic Batrachospermum-plants arise.
3. Frequently however, especially in conditions of feeble illumination, the pro-embryo develops more luxuriantly, tufts of erect cell-rows arise upon it—these have been described as species of Chantransia—and Batrachospermum-plants may also develop upon them, but if their primordia arise at too great a distance from the substratum they abort.
4. The pro-embryos may propagate themselves independently by means of gemmae (gonidia).
5. Secondary pro-embryos can develop from the cortical cells of the Batrachospermum-plant.

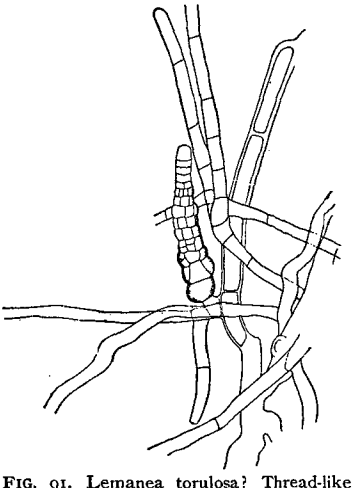

FIG. 91. Lemanea torulosa? Thread-like 'pro-embryo' upon which the plant destined to produce the sexual organs arises as a cell-mass. The condition is similar to what is found in mosses.

Here then we see that the pro-embryos are capable of an independent propagation, and that they are able to grow under conditions which do not suffice to call forth the higher form of development of the plant; these facts entirely correspond with what is known in the case of the Musci.

Of marine Florideae only two cases will be cited here:—

Dumontia filiformis[2] forms in germination an anchoring disc, consisting of vertical rows of closely compressed cells, which clings closely to the substratum, and resembles Hildenbrandtia, another genus of the Florideae. Upon the disc there is developed a branched erect thallus which dies after producing the fructifications, whilst the disc perennates and may produce new shoots of Dumontia. This then is

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[1] See Sirodot, Les Batrachospermes, Paris, 1884, and the criticism of his views in Flora, 1889, p. 5.

[2] Reinke, Algenflora der westlichen Ostsee. Kiel, 1889. Brebner, On the origin of the filamentous Thallus of Dumontia filiformis, in Linnean Society's Journal, vol. xxx, p. 436. I think the *endogenetic* origin of the thallus upon the disk, described by Brebner as a frequently occurring phenomenon, is due to its overgrowth at an early period of development.

fundamentally a similar relationship to that which we have seen in Lemanea and Batrachospermum.

Polysiphonia Binderi [1] exhibits peculiar features. The development of the plant begins with a cylindrical germ-shoot which altogether resembles that of the type of the genus in structure and configuration. Upon this one or many flat structures arise laterally, and these lay themselves like a crust upon the surface of other Algae, chiefly species of Codium, and may be regarded as composed of a number of threads of Polysiphonia united together in one plane. When the formation of propagative organs has to take place free threads of the Polysiphonia are again produced and they bear tetraspores. This case is specially interesting. It is clear that the crust-form of the thallus is a secondary adaptation which brings about the firm anchoring of the organ to the substratum; the adaptation does not appear however in the first stages of germination. Had the crust appeared in the germination of the spore, which it is quite possible to conceive, we should have had a case somewhat like that of Dumontia, but in that genus the structure of the disc points to the retention of a more primitive character.

Other Algae behave in a manner similar to those already described, but I must content myself here with a brief reference to them. The pro-embryo of Chara is described in every detail in the larger text-books [2]. In the Sphacelarieae [3] an anchoring disc is usually formed in germination upon which the cylindrical shoots which do the work of assimilation and bear the fructification are then produced. The anchoring disc is evidently made up of creeping cell-threads which are fused with one another as they are in Polysiphonia Binderi, and have therefore experienced further differentiation about which however I cannot pause to speak. Battersia mirabilis is specially interesting because the anchoring disc, which I regard as an adaptation arising secondarily [4], appears as the real vegetative body of the plant, and upon it the shoots bearing the fructification arise as short appendages in the same way as they do in Ephemerum, Lejeunia Metzgeriopsis, and others amongst the Bryophyta.

We see then in all these Algae that the juvenile stages exhibit two peculiarities either separated or together: on the one hand a primitive configuration which conforms with that of allied forms (Polysiphonia Binderi) or presumptive ancestors (Bratachospermum); on the other hand adaptations to which we cannot attribute a phylogenetic significance and which in these Thallophyta chiefly, although not always, stand in connexion with their fixation to the substratum.

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[1] This plant has been reckoned as the type of a special genus Placophora, because of its vegetative characters of adaptation, but this is opposed to all right principles of classification. See Flora, 1889, p. 3, where the literature is cited. Figures of this plant will be found in my 'Pflanzenbiologische Schilderungen,' i. p. 64, figs. 69, 70, 71.

[2] Goebel, Outlines of Classification, p. 53.

[3] See Reinke, Übersicht der bisher bekannten Sphacelariaceen, in Ber. der deutsch. bot. Ges. viii. p. 201; also Beiträge zur vergl. Anatomie und Morphologie der Sphacelariaceen, in Bibliotheca botanica, Heft 23, where the literature is quoted.

[4] Amongst Ectocarpeae a similar formation of anchoring discs occurs, but it is not general. See my 'Pflanzenbiologische Schilderungen,' i. p. 163.

2. BRYOPHYTA.

The few examples of the Bryophyta I have referred to above must suffice here for the group; the interesting phenomena of their germination will be described in full detail in the special part of this book.

I may however point out that the juvenile form, the protonema, is not the only interesting feature in their history: the similarity of the primary leaves of the young moss-plant, in species exhibiting a special adaptation in their adult leaves, with the simpler leaves of other mosses is another point worthy of notice. This happens in Sphagnum, Fissidens, Polytrichum.

3. PTERIDOPHYTA.

The development of the *sexual generation* will be treated of in detail in the special part of this book; here I have only to consider the juvenile stages of the *asexual generation* which are interesting in relation to the

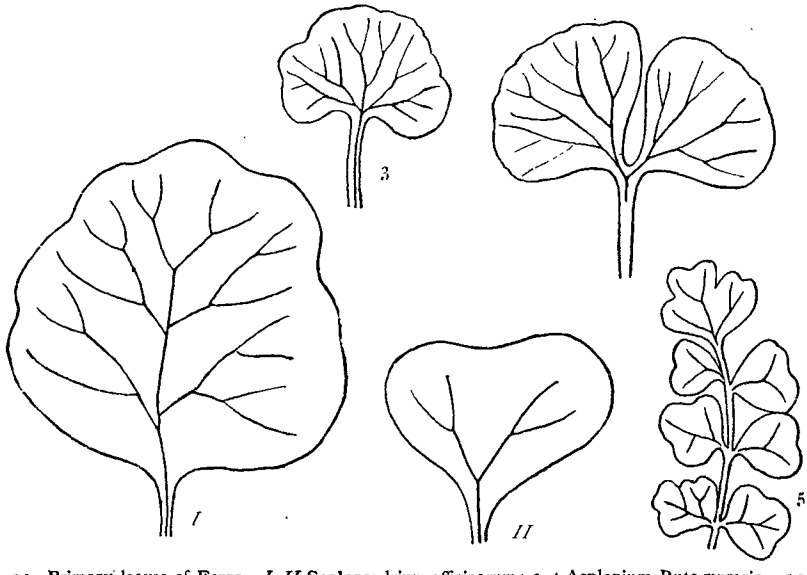

FIG. 92. Primary leaves of Ferns. *I*, *II* Scolopendrium officinarum; 3, 4 Asplenium Ruta-muraria; 5 old leaf of Asplenium viride. Magnified.

question now under discussion. The aquatic Pteridophyta will be mentioned along with the aquatic Angiosperms.

Equisetineae and Lycopodineae are essentially homoblastic in their development.

The ferns are, as is well known, distinguished by great diversity in the form of their leaves; the primary leaves however are uniform even in ferns whose adult leaves are very different from one another. Fig. 92 illustrates this. It gives a representation of the primary leaves of Asplenium Ruta-muraria and of Scolopendrium officinarum, two ferns whose adult leaves are as different as possible, those

of the former having a much divided surface, whilst in the latter they are elongated and undivided. The primary leaves in the two plants are nevertheless very similar. We observe that the primary leaves are traversed by forking nerves, and that the leaf-surface itself shows a tendency in many forms to dichotomy, but even where this is not the case the manner of growth of the leaves is alike. In the leaf *II*, belonging to Scolopendrium officinarum, a mid-rib, constructed sympodially out of the forking nerves, is visible, and as the leaf develops this always becomes more conspicuous, *I*; whilst this forking can be traced in the succeeding leaves, in many species where these take on gradually a pinnate form, the pinnules, at least at the apex of the most strongly developed leaves, appear more and more as lateral formations. This applies also to fern-leaves in which at an early period growth by an apical cell is replaced by growth by marginal cells[1]. In many ferns, Ceratopteris thalictroides for example, the apical cell is still present even when some of the pinnules are laid down, and the pinnules then doubtless represent *lateral* off-shoots of the primordium of the leaf. In such cases the primary leaves must evidently be considered as *arrested formations* in which the primitive growth by an apical cell has passed into growth by marginal cells at a much earlier period, before any branching has taken place[2]. It would serve no useful purpose to depict here the gradual passage to the adult leaves; two facts however must be mentioned:—

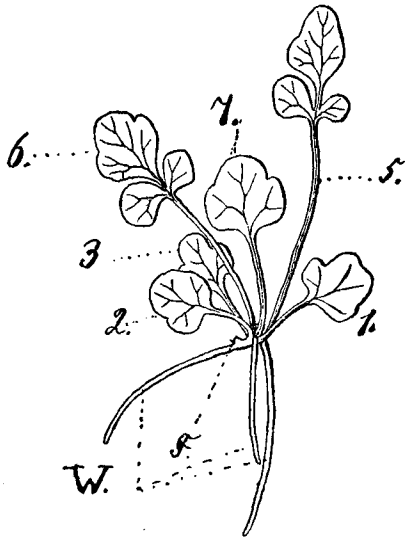

FIG. 93. Doodia caudata. Germ-plant. The leaves are numbered in the succession of their age. In leaves 5 and 6 the feathered configuration has been attained, but in leaf 7 there is a reversion to the configuration of leaf 2 in consequence of unfavourable environment.

1. The course of the development of the primary leaves, notwithstanding all external differences, conforms with that of the adult leaves—they are arrested formations.

2. In support of this we have in addition to morphological considerations the facts, that the construction of the primary leaves varies, and that the higher form of leaf is reached the more quickly, the stronger the germ-plant is; further, we have the result of experiments, for we can interdict the leaf-formation of an adult plant and bring about again the stage of the primary leaf if we place the plant under unfavourable conditions. Fig. 93 illustrates this. The germ-plant represented here has with leaf 5 reached the type of a feathered-leaf although only two pinnules are visible, but leaf 7 has taken on again the configuration of the primary leaves, of leaf 2 for example. In another experiment a plant which had reached the stage of a leaf with four pairs of pinnules produced thereafter one

[1] See Part II of this book.

[2] The primary leaves of Polypodium vulgare show no dichotomous venation; the apical cell is evidently retained for a long time.

with two pairs, and had its vegetation been continued under the unfavourable conditions it would have finally produced the primary leaf-form. In other experiments plants which had developed more than four pairs of pinnules went back to the stage shown in leaves 6 and 7 in Fig. 93. In old plants possessing stronger shoot-axes and abundant reserve-material, such a reduction is usually impossible because at the vegetative point primordia of leaves already exist the differentiation of which is determined, and because the plant has sufficient plastic material available to make it at first less liable to the influence of external unfavourable conditions.

4. GYMNOSPERMAE [1].

The seedlings of the Cycadeae furnish nothing special in their configuration for our consideration [2], but those of many Coniferae on the other hand have attracted much attention as many of them play an important part in horticulture. The juvenile form, especially in many Cupressineae, can be 'fixed,' that is to say, we can artificially prolong or make theoretically unlimited what is normally only a developmental stage more or less rapidly passed over. This can be effected in two ways [3]—either lateral shoots of the seedling which show the characteristic juvenile form are used as cuttings, or the chief shoot is removed above the basal lateral shoots and these then grow stronger and retain the juvenile configuration, whilst in normal circumstances they would have been suppressed by the stronger and differently formed chief shoot. Even at a later age the plant retains by preference at the basal region the capacity to produce shoots of a juvenile form. A few examples may be given here:—

1. Pinus. The pines produce as is known only brown 'scale-leaves' upon the shoot-axes which form the framework of the plant, and these scales act as bud-scales and fall off soon after the unfolding of the bud. Spur-shoots arise in their axils which bear two or many needle-like leaves; in Pinus monophylla there is only one. The seedlings however produce foliage-leaves upon the long shoots following the cotyledons. In Pinus Pinea this continues for many years [4], but in Pinus sylvestris the formation of primary leaves disappears in the second year, they are still formed at the base of the elongating shoot but scales take their place in its upper part, and in their axils the spur-shoots arise. It is stated in the literature that the juvenile form can be 'fixed' by cuttings, but I have not been able to satisfy myself upon this point as the cuttings did not grow in my experiments. The needle-like primary leaves have, according to Kaufholz [5], a simpler anatomical structure than the subsequent foliage-leaves; the provision

[1] See the papers by Carrière and Beissner quoted by me in Flora, 1889.

[2] The primary leaves of Ginkgo are arrested formations.

[3] The first method has been long known, the second was first brought into notice, so far as I know, by myself. It has special interest because it illustrates the influence of relationships of correlation. Normally the shoots showing the juvenile form are suppressed by those of the adult form; if the latter be removed the former grow more strongly and acquire a duration much longer than normal.

[4] The duration and degree of development of the juvenile form varies in the same species.

[5] Kaufholz, Beiträge zur Morphologie der Keimpflanzen. Inaug. Dissertation. Rostock, 1888.

for controlling transpiration especially is much less developed, as is to be expected in plants growing under the protection of others.

2. Larix. The juvenile form in this genus in its first, and occasionally also in its second year, shows a difference from the adult, inasmuch as the leaves persist during the winter as they do in species of the nearly allied genus Cedrus and in Pinus, whilst on the ordinary shoots they are deciduous.

3. Cupressineae. The formation of leaves in this group is very variable even within one genus. Juniperus communis for example has the typical form of leaf of the needle-leaved trees, namely, spreading needles. In Juniperus virginiana, species of Cupressus, of Callitris, of Chamaecyparis, and of Thuya, the leaves of the mature shoots are in great part 'concrescent' by their upper side with the upper side of the shoot; and the needle-leaves are restricted to the juvenile form. In male plants of Juniperus chinensis however twigs bearing needle-like leaves often appear upon old plants[1], the flowers however usually arise on the twigs which have adpressed scale-like leaves, although I have occasionally found them in the axil of needle-leaves. Twigs with needle-leaves which I used as cuttings seven years ago have now grown into bushes nearly 2 m. high, and these have retained their form of leaf but will likely produce later twigs with adpressed leaves. The juvenile stage in all the genera mentioned has spreading leaves and the plant can be fixed in this form, growing into high stems with quite a different appearance from that of the normally developed plants of the same species[2]. Such plants do not usually produce flowers and yet this may occasionally take place. I have elsewhere[3] referred to the instances of this which are described in the literature, and I have myself subsequently seen an example at the Lago di Garda. The juvenile forms of these plants (and the same is the case in Pinus) must undoubtedly be considered as the more primitive and we have thus been able to revive to a certain degree their *stem-form!* That the fixed juvenile forms retain their configuration and are usually unable to produce sexual organs, although external conditions are quite favourable for this, when they have attained an age and a size at which the normal plants are and have been for long sexually mature, is an extremely interesting feature of the development. Between juvenile forms and adult forms there are naturally transitions and these can be fixed, but under favourable conditions pass over more or less quickly into the adult form.

It is probable, especially from the analogy with cases which will be mentioned immediately, that in the Coniferae which have been described above, the duration of the juvenile form of uninjured individuals can be prolonged by definite external influences. The experience of different breeders has led Beyerinck to say[4] that 'all circumstances which prejudice nutrition favour the retention of the juvenile character,' and consequently the juvenile form is retained longer when plants are

[1] See Goebel, Pflanzenbiologische Schilderungen, i. Fig. 11.

[2] These juvenile forms are known in gardens as species of Retinispora, and gardeners have maintained that they remain small and do not reach a great age. This is not however everywhere true (see my papers cited at the beginning of this section); and yet we need not be surprised if plants produced from cuttings have a root-system less developed than the normal, and if the leaves of the juvenile form being softer are less resistant than the adult ones.

[3] Goebel, in Flora, 1889, p. 36.

[4] Beyerinck in Botan. Zeitung, 1890, p. 539.

cultivated in pots. It is possible that the Japanese have obtained their forms of Retinispora by cultivation in pots, accompanied by root-pruning, whereby they have hindered through unfavourable conditions the appearance of the adult form.

The behaviour of only two other genera of conifers in which the organs of vegetation are especially diverse will be mentioned here.

4. Phyllocladus[1]. The species of Phyllocladus are distinguished by their leaf-like twigs, phylloclades, standing in the axils of small scale-like leaves which, originally green, soon become withered and brown. These scale-like leaves are merely transformed primordia of foliage-leaves and they are, as it were, a middle stage between the normal occurrence in the Coniferae and that which is seen in Pinus, where the leaves on the chief-stem are from the outset brown scales. The first leaves of the first annual shoot of the seedling, as well as a portion of those which are developed in the second year, are flat green needles; at the end of the shoot they are much shorter; and on the third annual shoot they are much more like the scale-leaves of the older plant, and into these they gradually pass. The phylloclades too only gradually acquire their striking leaf-like configuration, and occasionally their extremity develops into a cylindrical twig clad with leaves arranged spirally. A 'fixation' of the juvenile form has not yet been tried.

5. Sciadopitys. The germination in this genus is quite like that of Pinus, but at a later stage it forms its peculiar double needles, not spur-shoots. After the two linear-lanceolate cotyledons foliage-leaves appear on the short first annual shoot of the seedling plant. These leaves are simple with an undivided apex and have a simple vascular bundle. Upon the next annual shoot the leaves are reduced, as is the case in Pinus, to scales and in their axils in the upper part of the shoot are developed the characteristic double needles with retuse apex and having two vascular bundles.

5. ANGIOSPERMAE.

The differences in the construction of the juvenile and the adult form are in general the greater the more different are the external conditions to which they are severally adapted[2], whilst if these do not operate, the primary leaves, with which we have here at first to deal, are only arrested formations[3], if they are specially different from those which follow, and their differentiation is then simpler. Thus the primary leaves are simple in the trifoliate species of Trifolium and in Ononis and other genera, and this primary form of leaf is retained for a very long time in Ononis Natrix. Kennedya rubicunda has primary leaves without trace of pinnules, then follow leaves in which pinnules are laid down but are reduced to small pointlets[4]; on succeeding leaves pinnules are

[1] H. Th. Geyler, Einige Bemerkungen über Phyllocladus, in Abhandl. d. Senckenb. Naturf.-Gesellsch., xii (1881), p. 209.

[2] See what has been said on page 144.

[3] As I have shown to be the case in the ferns, see page 152.

[4] This is also observed in the lowermost pinnules in old plants of Acacia lophantha, which I mention here because it shows the phenomenon is one of arrest.

fully developed[1]. The primary leaves of Vicia Faba differ greatly in configuration from the succeeding ones; they are reduced to small three-toothed leaflets, the middle tooth representing the leaf-blade, the lateral ones the stipules. The primordium of the leaf has remained stationary here at a very early stage, and in subsequent leaves experiences only an increase in size and no further morphological differentiation takes place. We can prove this experimentally. The axillary shoots which spring from the base of a plant all possess the same form of leaf. If the chief shoot be removed above the primordium of a lateral shoot, this will be forced to shoot out at an early period, and instead of the primary leaves there will be found upon it according to the degree of development to which it

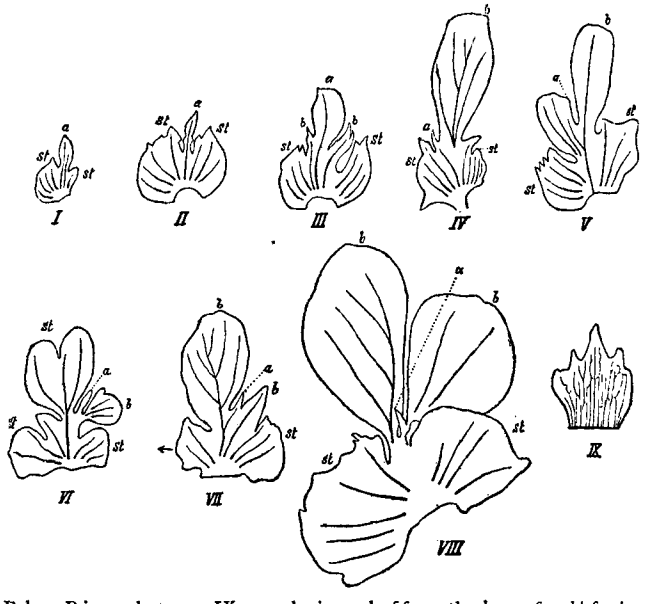

FIG. 94. Vicia Faba. Primary leaves. *IX* normal primary leaf from the base of a chief axis. *I-VIII* different stages of transformation of primary leaves at the base of a lateral shoot, obtained through the removal of the chief shoot; *a* leaf-apex, *st* stipule or its vestige, *b* lateral pinnule. The venation is not completely represented.

had already attained the most varied intermediate forms between the primary leaves and the foliage-leaves or typical foliage-leaves (Fig. 94).

This kind of case shows us also that the developmental arrest of the primary leaves stands in correlation with the formation of other organs of the same plant. It is clear moreover that the leaves which are first developed upon a plant and which stand near the ground can more easily bear the want of a higher differentiation than the following ones which are exposed to the wind, rain, and other external factors.

These differences in external relationships appear still more strikingly when we look at groups of plants marked by common biological features.

[1] Further examples will be found in Flora, 1889, p. 29.

A. Climbing Plants.

1. ROOT-CLIMBERS.

The configuration of the juvenile leaf and of the adult leaf is very different in many climbing species of Aroideae. I myself examined this difference in an aroid, probably a species of Monstera or Philodendron, which climbed up the trees of Erythrina protecting a plantation of cacao in Venezuela (Fig. 95). The earlier leaves are sessile or very shortly stalked and lie closely adpressed to the surface of the stem, and thus protect the young anchoring roots of the plant. Subsequently the form is changed; the leaves acquire a larger lamina and a longer stalk and stand out from the stem, until finally the large leaves with cut margin are produced which are characteristic of the mature plant. The aroid cultivated in gardens as 'Pothos celatocaulis' is undoubtedly a juvenile form of this kind, the mature stages of which are not known, although the plant often reaches a length of many yards (Fig. 96).

FIG. 95. Young plant of a climbing species of Aroideae. The lower leaves are closely adpressed to the stem of the tree upon which the plant grows as is the case in 'Pothos celatocaulis,' the upper leaves have another form. From a photograph taken at San Estéban, Venezuela.

FIG. 96. 'Pothos celatocaulis.' Juvenile form. The distichously leaved shoot grows upon the stem of a tree-fern to the surface of which the leaves of the aroid are adpressed.

Ridley[1] has pointed out that Pothos flexuosus, so much cultivated in gardens, is in like manner the juvenile form of 'Anadendrum medium,' and we may be the less surprised that this has not been noticed before seeing that in this plant all its forms of leaf only seldom occur together[2], and many individuals persist for a long time in the juvenile stage. The forms of leaf are represented in Fig. 97. The following is Ridley's description:—

A. The leaves are of a velvety green and stand in two rows close together. If the plant grows higher they become broader and more ovate, less oblique, cordate at base, and are evidently stalked and attain a length of 7·5 cm. and a breadth of half as much.

FIG. 97. Anadendrum medium ('Pothos flexuosus'). Different forms of leaf. *A* unstalked 'velvety leaves'; *B* thicker leaves from higher up the stem; *C* the leaf-stalk now begins to appear; *D-G* further stages of differentiation, *G* is a leaf from a flowering plant; *H* leaves of a 'stolon.'

B. Still higher up they attain a length of 18–20 cm. and a breadth of 10 cm., develop a long point and a short thick stalk of 2·5–4 cm.

C. We next find them still in two rows and lying flat upon the stem of the supporting tree, but now they have become pointed ovate with a cordate base, and are 15–20 cm. long and 10 cm. broad, with a stalk 10 cm. long.

D. The distichous arrangement is now lost and the leaves no longer lie upon the stem but spread out in all directions; their dark shining green shows that they are very different from the delicate velvety green leaves of the lower region, and whilst the outline and size of the preceding leaves are retained, indications appear of feathered segmentation.

E. The stalk has now a length of 20 cm. and forms a 'knee' close to the lamina, which latter has a length of 20 cm. and is cut in a feathered manner almost to the midrib, whilst on both sides of the midrib a number of elliptic perforations are found.

F. The lamina of the leaf has attained now a final length of over

[1] Ridley, in Gardeners' Chronicle, ser. 3, vol. i (1894), p. 527.

[2] In the aroid figured in Fig. 95 this commonly happens.

40 cm. with small segments 2·5–4 cm. long, similar to what we find in the leaf of Rhaphidophora.

G. The form of leaf is that of the plant that is ready to flower; another form has yet however to appear.

H. Long pendent stolons often arise which possess broad oblong or almost round leaves, cordate at their base and nearly sessile.

If the Pothos-form grows upon a rock or a wall the higher development does not take place [1], but on a tree-stem it can and usually does develop into the Rhaphidophora-form when it has grown higher. Cuttings of the Rhaphidophora-form never revert to the Pothos-form, but both forms develop into the long pendent stolons with round widely-separated leaves when they grow out beyond their support. According to Ridley the development of the Rhaphidophora-form has nothing to do with light as it frequently appears in dark parts of the forest, whilst the Pothos-form does not develop further upon a rock or a tree-stem exposed to the light; but perhaps there are wanting here the other factors necessary to normal growth, such as moisture, and the juvenile condition of the plant is therefore retained as happens in the Coniferae referred to above. It would be of great interest were this examined experimentally. The allied species Anadendrum marginatum and Anadendrum montanum have no juvenile form of this kind.

Some climbing plants belonging to other families behave like these aroids, and the resemblance with Marcgravia is so complete that their juvenile forms have been often confounded in gardens [2]. The species of Marcgravia are amongst the most striking climbing plants of the tropical American flora. The juvenile form possesses plagiotropous shoots the leaves of which adpressed to the tree-stems cover the roots, but non-rooting shoots arise later which are either orthotropous or at least stand out from the substratum and bear stalked larger leaves, and it is upon these that the flowers arise [3]. Some climbing species of fig, Ficus scandens and F. pumila for example, exhibit like features and in our plant-houses we see them almost always in their plagiotropous juvenile form.

The juvenile form shows in all these plants an evident adaptation which has arisen in conjunction with their climbing mode of life, and we see the

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[1] The history of the ivy leads me to doubt the general validity of this statement; at least it is difficult to see why such a difference should ensue.

[2] I have often had sent to me by nurserymen the juvenile form of an aroid as a Marcgravia. Some of the Marcgravieae seem to have no juvenile form, for example, Norantea guianensis.

[3] The different forms of leaf differ anatomically. Upon the under side of the leaves of plagiotropous shoots there is a relatively thick air-tissue into the inter-cellular spaces of which water is perhaps frequently injected, and it forms a protective covering to the roots. If the plant grows upon a thin supporting branch the surface of the leaf curves round in correspondence with the surface of the branch. As in the climbing aroids referred to in the text the juvenile leaves in Marcgravia are distinguished by their 'velvety' character; a drop of water placed on the leaf rapidly disperses.

same in the ivy whose young shoots are plagiotropous with the leaves in two rows, and in this respect differ from those of allied Araliaceae. In the ivy however the *form of leaf* of the juvenile shoot, which has 3–5-lobed leaves whilst in the orthotropous flowering shoots the leaves are ovate (Fig. 98), cannot at first be brought into connexion with the external relationships; and the attempts which have recently been made to establish a relationship between the pointed form of the leaves of the juvenile shoot and their combination into a 'leaf-mosaic' does not help us; such mosaics are, as unprejudiced observation of nature shows, either inventions, or exceptional cases picked out with the intention of proving the conformity of the form of the leaf with its purpose. The ortho-

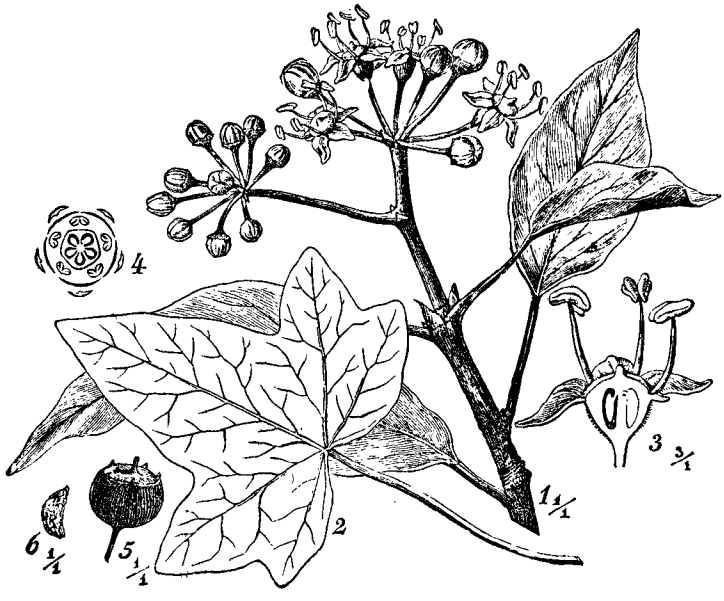

FIG. 98. Hedera Helix. 1 portion of a branch ending in an inflorescence. The form of leaf upon it is different from that (represented at 2) upon the sterile branch. After Wassidlo. Lehrb.

tropous radial shoots with a $^2/_5$ phyllotax, which is also $^5/_8$ and $^8/_{13}$, appear in ivy only after a certain age is reached and are then probably only formed if light of a higher intensity is available than is required for the formation of the plagiotropous shoots. The first leaves which appear in germination are like those of the orthotropous shoots although the seedling has its leaves from the beginning in two rows; the five-lobed leaves appear only in the second year[1]. The radial shoots are frequently used in horticulture for cuttings and these may grow up and live for a long time as 'tree-ivy[2]'; they occasionally develop at their base shoots which revert to the juvenile form.

[1] Buchenau, in Botan. Zeitung, 1864, p. 236. [2] Mistakenly designated var. 'arborea.'

Juvenile forms then occur in the climbing plants we have mentioned, and they are distinguished by their plagiotropous growth and its consequent different form of leaf, frequently also by a different phyllotaxy. We have already seen above on page 94, in Vaccinium Myrtillus, how in plagiotropous shoots arising from radial ones the $^1/_2$ phyllotaxy may develop; in the case of these climbing plants this change of position has become inherited.

2. PLANTS WITH TENDRILS.

Most tendrillous plants have in their juvenile state no tendrils at all or only functionless ones. The latter fact is of interest because it brings again under our notice the *arrest of organs*.

Let us first of all consider *leaf-tendrils*. We shall find here in many instances that the young plants show all transitions from the first foliage-leaves, which are not tendrillous, to those in which the tendrils diverge in their configuration from that of the foliage-leaves and have taken on the form of thin sensitive filaments. There are examples of this in Corydalis claviculata, Adlumia cirrhosa, and others. In the remarkable germination of Nepenthes[1] we can follow clearly how the leaf, constructed primarily only as a trap for animals and organ of assimilation, gradually becomes also a climbing organ. On the other hand in Cobaea and in the Leguminosae the transition is an abrupt one.

Lathyrus Aphaca may be cited as an example remarkable in more than one respect (see Fig. 76). The whole leaf-lamina has here been transformed into a tendril. Upon the seedling plant some simple primary leaves follow the hypogeal cotyledons as is the case commonly in Leguminosae. The first of them is usually a leaf without any segmentation or with only a hint of this; then come several three-pointed green scales, the middle point corresponding to the lamina of the leaf, the two lateral ones to the stipules. Next come foliage-leaves each of them with two pinnules and asymmetric stipules. In the following leaves the leaf-lamina is arrested and is seen as a small point between the greatly enlarged stipules which are now symmetric. In all the succeeding leaves the lamina is transformed into a tendril. These rudimentary leaves must be considered as the first functionless tendrils. We may assume that in Lathyrus Aphaca the formation of leaves was originally as in other species of Lathyrus, that only the terminal portion of the leaf had the function of a tendril, that the pinnules were then suppressed and in consequence of this the stipules attained their exceptional size.

The formation of leaves in Lathyrus Ochrus[2] is very peculiar and

[1] Goebel, Pflanzenbiologische Schilderungen, ii. p. 98.

[2] Lathyrus Clymenum and L. mauritanicus show the same features.

the plant has given rise frequently to discussion because a series of processes are here commingled (see Fig. 99). The first leaves are small and lanceolate; and at the base of each a membranous tooth, or it may be two such teeth, are distinguishable which are to be regarded as the arrested stipules. As the leaf becomes larger its apex grows out into a tendril which at first is rudimentary. Right and left of it, or perhaps only on one side, a further differentiation takes place and two lateral tendrils appear. These are seated then upon a broad leaf-surface. Subsequently pinnules appear and the uppermost leaves have a bifid or trifid terminal tendril with one or two pairs of pinnules below it; not infrequently a tendril may be observed opposite one of the pinnules. How are we to explain this peculiar construction[1]? Irmisch considered the flattened portion of the leaf to be a leaf-stalk. This is however opposed to the history of development and to what we find in other Leguminosae.

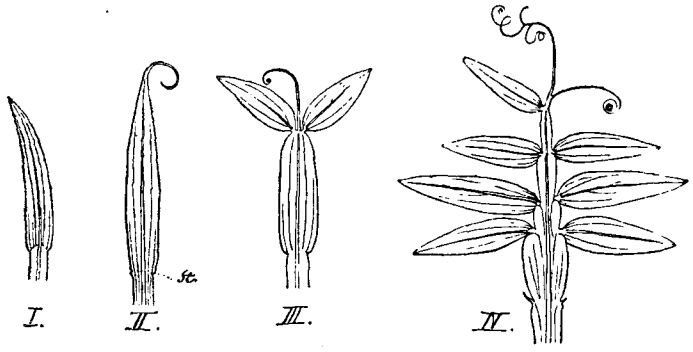

FIG. 99. Lathyrus Clymenum. Forms of leaf from a seedling at different ages. *I* unmembered primary leaf; *II* primary leaf ending in a tendril, *st* rudimentary stipule; *III* and *IV* leaves upon which pinnules have appeared.

In them we commonly find primary leaves of the form represented in Fig. 94, *I*, and these are certainly arrested formations, as I have experimentally proved—*a* is not a leaf-stalk without a blade but corresponds to the whole upper portion of the primordium of a leaf, the so-called upper leaf; a leaf-stalk is generally not yet developed. If we imagine the portion marked *a* to be greatly increased and the portion immediately below it to be only slightly developed, then we should arrive at a condition as we find it in Lathyrus Ochrus (Fig. 99, *I*). In this species however the leaf-formation remains long at this stage; the surface of the leaf is then not a leaf-stalk[2] but the whole of the upper part of the primordium of a leaf no longer sharply separable from the lower

[1] An account of the development of leaves ought properly to precede the discussion of this matter, but that falls into the special part of this book and I cannot for other reasons omit this peculiar case here.

[2] Schenck, Beiträge zur Biologie und Anatomie der Lianen, i. p. 184, brings forward again the explanation given by Irmisch, but overlooks all developmental facts.

portion or leaf-base. Subsequently development proceeds in the way above described. The arrest of the stipules has certainly a causal connexion with the broadening of the whole primordium of the leaf; they have become superfluous as protecting organs for the stem-bud because this function is performed by the broad leaves themselves. The broadening of the leaf-surface will however allow the plants to grow up quickly and to overcome their rivals, and I should suppose that these species grow upon densely clothed grassy spots, or in hedges, in not very strong illumination. In this way I believe we can follow the changes which have taken place here.

Lathyrus Nissolia behaves in the same way, only in it the uppermost leaves develop no tendrils; the seedling produces, as in Lathyrus Ochrus, small lanceolate simple primary leaves provided with rudimentary stipules. There seems to me to be at the present time no positive foundation for Darwin's hypothesis[1] which derived this species from an original twining plant which became a leaf-climber, then lost the branching character of its tendrils, and finally also their capacity for rotation and their sensitiveness, with the result that the tendrils again became leaf-like. Darwin assumed also a double change in the construction of the stipules. It is possible that Lathyrus Nissolia sprang from a tendrillous plant, but I do not see any advantage in assuming so complex a path of development as Darwin does; a comparison with Lathyrus Ochrus seems to me to indicate a much simpler one.

I may in conclusion cite one more case which derives interest from the peculiarity that the primary leaves have the function of tendrils. Darwin has shown[2] that Tropaeolum tricolorum produces no leaves up to a height of two to three inches; it only bears 'filaments,' sensitive to contact, which in the upper part of the stem pass over into complete leaves. These 'filaments' are merely primary leaves, and their taking on the function of tendrils is evidently due to the extreme thinness of the shoot-axis which necessitates the production of supporting organs at a much earlier period than is the case with other plants bearing tendrils. The seedlings of the plant which I examined produced only few 'filaments' before formation of complete leaves occurred. The filaments are elongated primordia of leaves upon which no separation into stalk and blade has as yet taken place. Higher up on the plant a blade becomes visible. A feature exhibited by Tropaeolum majus may be here briefly mentioned. Whilst most species of the genus have no stipules, although they evidently possessed them originally, Tropaeolum majus has them on the first two leaves but with a reduced character; sometimes one is wanting and they do not always appear in the normal position.

[1] Darwin, Climbing Plants, p. 154.

[2] Darwin, l. c. p. 47.

In the special part of this work I shall treat of the Cucurbitaceae which bear tendrils and I will only mention here that, as I have elsewhere shown [1], the formation of simple tendrils characteristic of the seedling may appear in adult plants if they are badly nourished.

B. Aquatic and Marsh Plants.

Only a few of these are briefly referred to here because I have so fully dealt with many of them elsewhere [2].

The primary leaves of all the Sarraceniaceae are essentially alike in their configuration whilst the later ones are often markedly different from one another. The features exhibited by the seedlings of Utricularia are of special importance because they show a complete conformity between the whole construction of the land-species and the water-species which subsequently are widely different from one another. An adaptation which renders difficult the overturning of the embryo-plants is visible in the configuration of the peltate primary leaves of Salvinia and the turbinate ones of Azolla [3]. The peculiar submerged primary leaves which appear in many Nymphaeaceae must be considered as arrested formations; the floating leaves arise later, but their formation may be entirely suppressed in Nuphar if the conditions are unfavourable, so that the plant persistently forms leaves which correspond with those of the seedling.

The behaviour of some monocotyledonous plants has given occasion for a different explanation. All of the Alismaceae, Pontederiaceae, and Potamogetoneae which have been as yet examined, no matter how different the adult form of their leaves may be, agree in the production in germination of simple band-like leaves which were formerly erroneously called phyllodes. By intermediate stages they pass into the higher form of leaf which is provided with a stalk and blade. The primary form of leaf is retained by individual species for a varying length of time; for the longest period by those which live more submerged. Amongst these, for example Heteranthera zosteraefolia and Sagittaria natans, the higher form of leaf only appears on the flowering plants and then only in a few leaves, whilst numerous band-like leaves are present; on the other hand these band-like leaves are found in the species more adapted to a land-life only as a stage of development rapidly passed over. Differences of this kind are found even in species of the same genus, as a comparison of Sagittaria natans and Sagittaria cordifolia shows, for in the latter species the primary leaves play only a subordinate part.

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[1] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, p. 240.

[2] Goebel, Pflanzenbiologische Schilderungen, ii. Numerous figures will be found in this work.

[3] See Fig. 73 in my 'Pflanzenbiologische Schilderungen,' ii.

The question we may now ask is—do these primary leaves exhibit a form of leaf which has arisen through adaptation to life in water, or do they not? Whilst there can be no doubt that there is a connexion between the number of these leaves and the mode of life of the plants to which they belong, yet the fact that in a large majority of other monocotyledonous plants the band-like form of leaf is typical and that these leaves are able to adapt themselves to a land-life, taken along with other circumstances, led me early to the view that there is no sufficient foundation for the assumption conveyed in the first part of the above question.

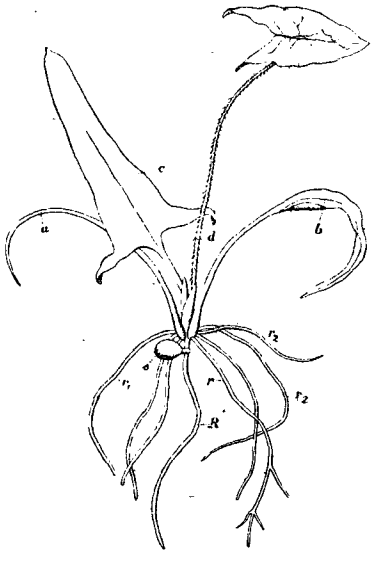

FIG. 100. Victoria regia. Seedling plant. The leaves are lettered in the order of their succession. *s* seed-coat; *R* chief root; *r*, r_1, r_2 lateral roots. After Trecul.

The submerged primary leaves in some dicotyledonous plants also have a simpler construction than, and present a configuration different from those which appear above the water. In Fig. 100 a seedling of the nymphaeaceous Victoria regia is represented upon which the first floating leaf *d*, which differs from those following it, has been already formed; the three preceding leaves are submerged ones, and in *a* the leaf-blade is not yet marked off from the stalk; in *b* and *c* its configuration is different from that of *d*. We have here to do with peculiarly developed arrested formations, and this is shown by the fact that the shoots formed upon tubers of Nymphaea rubra bear primary leaves like those of the seedling, and that under unfavourable conditions of growth, such as, for example, very deep water, Nuphar luteum remains for a long time at the stage at which water-leaves are formed similar to those produced in germination.

C. XEROPHILOUS PLANTS.

Plants of this description live in localities where they are at times exposed to the danger of too great transpiration, and they frequently possess, as is well known, adaptations to their habitat[1] which are expressed chiefly in diminution of the size of the leaf or in the formation of leaves with a vertically expanded lamina, as in Eucalyptus, and in the phyllodes of Acacia. When the shoot-axis of xerophilous plants has to do the work of assimilation instead of the leaves, it is usually broadened out.

[1] So conspicuous are these that they have in recent years been described *ad nauseam*.

The juvenile stages often show relationships different in character from those of the adult and conform in their configuration with plants which are not xerophilous, particularly in having well-developed leaves, although this is not always the case. The development of the leaves in the seedlings of Cacti, Casuarina, Ruscus aculeatus, R. Hypoglossum, and other plants, is not essentially different from that in the adult, but differences in this respect are seen even on nearly allied forms; thus the seedling of Ruscus androgynus possesses large well-developed foliage-leaves which are not produced on the older plants where the leaves are reduced to small scales. It has been pointed out above that the absence

FIG. 101. Ruscus aculeatus. Shoot. On the leaf-like phylloclades, *cl*, flowers are developed, *bl*; *f* axillant leaf. Lehrb.

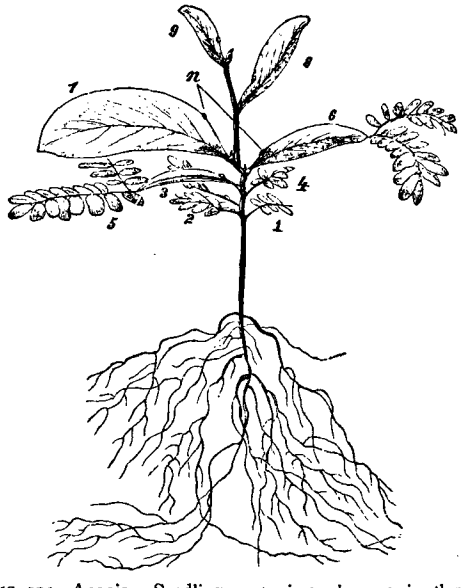

FIG. 102. Acacia. Seedling. 1–4 primary leaves as in other species of Acacia; 5 and 6 show transitions to phyllodes; 7–9 phyllodes; *n* nectaries. Lehrb.

of xerophilous characters in such juvenile forms is connected with the growth of the seedling plants under the protection of others, and that the development of such seedlings only takes place as a rule when sufficient moisture is present, whilst the further development of the plant is associated with claims of another kind. The following is a series of examples:—

1. The best known and most frequently quoted are the species of Acacia which produce phyllodes. The phyllodes arise by the broadening in a vertical direction of the leaf-stalk, sometimes also of the leaf-midrib, whilst the lamina aborts. Seedling plants (Fig. 102) however have without exception, so far as they have been examined, leaves which are like those of the species—possessing a bipinnate lamina and a normal leaf-stalk. As successive leaves are formed the leaf-stalk gradually broadens whilst the

lamina is reduced until the form of the phyllode is attained. In some species foliage-leaves may again appear after the phyllodes, for instance in Acacia heterophylla.

2. The features of Eucalyptus recall in some degree those of Acacia. In Eucalyptus there are no phyllodes on the older plants, but pendant leaves with a knife-blade-form and showing similar structure on both sides are distributed over the axis of the shoot. The seedling on the other hand forms oval dorsiventral opposite and decussate leaves for a long time on its four-angled twigs. The two stages of development have thus an entirely different aspect.

3. Many dicotyledonous plants exhibit much the same phenomena as those I have depicted in the case of many Cupressineae[1]. Some New Zealand species of Veronica, such as V. cupressoides and V. lycopodioides, show in quite a striking manner the habit of the Cupressineae with scale-like adpressed leaves. The seedlings of these species, so far as they are known, all have spreading leaves which possess a stalk and blade like those of other species of Veronica; but this differentiation disappears in the leaves which appear later. We may assume a similar behaviour for Melaleuca micromera, a cypress-like myrtaceous plant, on account of the phenomena of reversion[2] it exhibits. Passerina hirsuta[3] also has in its young condition spreading leaves whilst the subsequent ones are adpressed; other species of Passerina however only possess the spreading leaf corresponding with the juvenile form of P. hirsuta.

4. Plants in which the adult leaves are arrested:—

Zilla myagroides, a cruciferous plant possessing shoot-axes containing chlorophyll and constructed as thorns, has only arrested leaves, whilst in its juvenile stage there are large well-developed leaves[4].

Clematis afoliata exhibits a gradual reduction of the leaves upon the seedling plants aud the newly formed shoots.

Carmichaelia stricta possesses flattened shoot-axes with arrested leaves but shoots which proceed from its base behave as does the seedling plant. There appears upon the seedling plant after the cotyledons a simple undivided primary leaf just as in other Leguminosae which have been already referred to; following this comes a trifoliate leaf, and next a few imparipinnate leaves with two to three pairs of pinnules, and then the formation returns either to a trifoliate leaf or to a simple one, and higher up on the flat stem the leaves are reduced to small scales. The formation of leaves attains in the pinnate foliage-leaves its highest point and then again sinks. The conformity of the primary leaves with those reduced ones which appear *after* the pinnate foliage-leaves shows very

[1] See page 154. [2] See page 172.

[3] See the figure by Pasquale in Plate 1 of his book 'Sulla eterofillia.' Napoli, 1867.

[4] Goebel, Pflanzenbiologische Schilderungen, i. Fig. 3.

clearly that the primary leaves take origin through the same processes. In Carmichaelia Engsii *simple* foliage-leaves alone appeared on the seedling plant, and these in many examples were reduced to unstalked small scales, so that we have here in one genus the transition from heteroblastic to homoblastic germination.

Bossiaea rufa exhibits the same kind of germination as Carmichaelia stricta. The chief axis of the seedling produces a number of stalked oval leaves and is not broadened out. It is subsequently arrested, whilst out of the axils of the cotyledons and beneath them shoots develop which gradually become phylloclades. On these flat shoots the small pointed stipules only of the leaves remain, the primordium of the blade is arrested [1]. Other species of Bossiaea possess also flat twigs with well-formed leaves, for example, B. heterophylla, or cylindric twigs with foliage leaves, for example, B. microphylla [2]. We thus find in *one* genus all stages of transition.

Ulex europaeus, in which the leaves in the mature plant are transformed into thorns, possesses on the seedling plant after its first primary leaves trifoliate foliage-leaves like other Genisteae. The lateral leaflets on the leaves standing higher up on the stem gradually diminish in size and at last do not develop. The leaf now becomes simple and linear, is gradually transformed into a thorn, and at the same time the twigs also develop as thorns.

Colletia likewise deserves notice here [3]. The species of Colletia form spinose shrubs and the older plants bear small deciduous leaves. In C. cruciata the thorns, which are the lateral shoots, are strongly flattened. The seedling plants of all the species of Colletia known to me are constructed exactly alike; they have cylindric shoot-axes with well-developed foliage-leaves and the flattening of the shoot-axes in C. cruciata only takes place later. The configuration of the seedling plant proves itself here also to be a primary character.

Cacteae. The behaviour of Colletia cruciata finds an analogue in that of many Cacteae. The formation of foliage-leaves does not take place in the seedlings of the Cacteae, the leaves are here transformed into scales or spines, but the shoot-axes frequently show more primitive relationships of configuration than appear in the older plants. We may consider the following construction of the vegetative body as 'typical' for the majority of the leafless Cacteae—fleshy shoots invested by chlorophyll-tissue and bearing tufts of spines in the axil of small scale-like leaves. The spines are transformed leaves which arise upon very much

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[1] Hildebrand's statement that 'there is no trace of the leaf-blade' is certainly wrong.

[2] Askenasy Botanisch-Morphologische Studien. Frankfurt a. M. 1872, p. 4.

[3] For a Figure see Goebel, Pflanzenbiologische Schilderungen, i. Fig. 8.

reduced lateral shoots standing in the axil of the leaves. In many plants these tufts of spines are arranged on vertical ribs of the stem and this may be designated the 'Cereus-form.' From this form diverges in a very striking manner that which has a flat leaf-like shoot-axis as we see in many species of Epiphyllum, Rhipsalis, and Phyllocactus[1], and which may be termed the 'Phyllocactus-form.' If the history of germination be followed it will be found that the seedling plants have mostly a form which is like that I have described as the 'typical' configuration, although

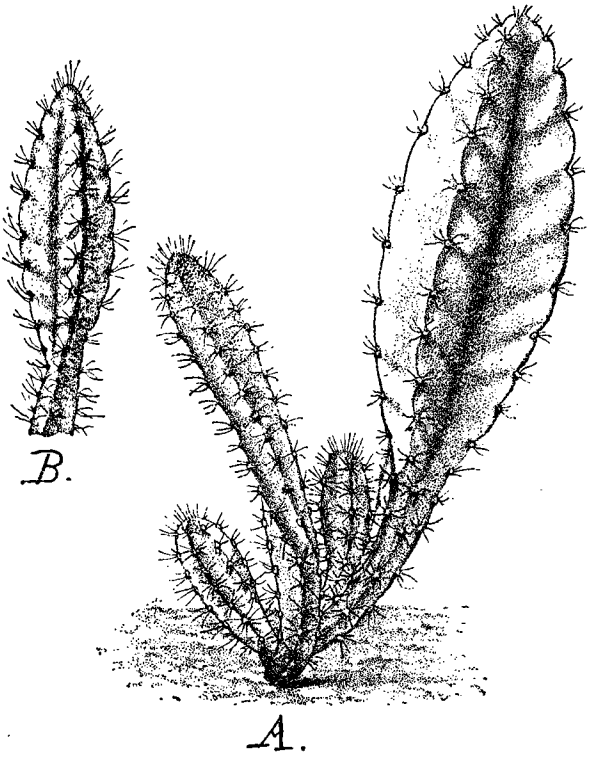

FIG. 103. Phyllocactus phyllanthoides. Seedling plant. The shoots are at first many angled and Cereus-like, but in the youngest shoot the number of the angles is reduced to three; the angles are wing-like. Later only two angles are found.

in different degrees in the different species, and we can follow in the seedlings how a transformation of form is brought about. Fig. 103 represents a seedling plant of Phyllocactus phyllanthoides which possesses a tetragonal shoot-axis beset with tufts of thorns on the ribs, and has quite the appearance of a Cereus. As the plant grows only two of the ribs remain, the shoot-axis becomes greatly flattened, and out of what was a 'Cereus-form' there is developed the apparently far removed 'Phyllocactus-form.' Other species also of the same genus show in germination

[1] Phyllocactus is only distinguished from Cereus by its habit.

a four-ribbed shoot, but two of the ribs are quite rudimentary and have the form of tufts or spines over the interval between the cotyledons, so that casual observation might lead one to suppose that the seedling had from the first two ribs; this is what happens in Phyllocactus Phyllanthus. The same appearances are presented, as I have shown, in species of Epiphyllum and Rhipsalis with flat shoot-axes. In those Cacteae also which do not subsequently flatten their shoot-axes 'Cereus-like' shoots appear in germination, and this is of the greatest interest from the phylogenetic point of view. Rhipsalis Cassytha and Rh. paradoxa are two species growing upon trees which in the adult state are as unlike as possible. The former has long thin spineless shoots, the latter has limited alternately three-ribbed shoots. The seedlings of both species are alike in their chief features, apart from mere points of size, and exhibit the ribbed spinose shoots which we have called 'Cereus-like'[1].

It would take me too far to speak of other examples of the Cacteae; many of these will be found in my 'Pflanzenbiologische Schilderungen' to which I have referred. The instructive exhibition by the seedling plants of the Cacteae of the development of different forms of the vegetative body out of a common basal form may perhaps be connected with the fact that in this group we have, as it appears, a phylogenetically recent family in which a sharp separation of the genera has scarcely yet taken place.

SUMMARY.

In the development of plants from the germ, be this spore or seed, there appear frequently relationships of configuration which are different from those exhibited by the adult plant, and this is chiefly the case when the seedling is adapted to other conditions than those which surround the subsequent stages of development. The configuration of the primary stages may be different within one genus and may vary also in one species.

In one series of cases, as is shown by comparison with allied forms, these must be considered as original forms relatively to the adult ones, and as becoming subsequently adapted to changed relationships. Thus the seedling plants of species of elm, beech, and hornbeam, constructed out of sympodially developed dorsiventral shoot-systems, are orthotropous and radial, as is the case in allied forms throughout their whole life. The seedlings of xerophilous plants do not exhibit the characters which are associated with a xerophilous mode of life; and the same may be said of plants climbing by tendrils and of other forms.

On the other hand, the juvenile states in many instances are undoubtedly those which have been changed by adaptation, as in Hedera, Marcgravia, Salvinia, and others, and frequently the seedling exhibits in

[1] See the figure of the habit in my 'Pflanzenbiologische Schilderungen,' i.

the formation of its organs, and especially in the formation of its leaf, simply an *arrest* which is probably a consequence of relationships of correlation.

Reversion to the Juvenile Form.

Special interest attaches to the fact that many plants are able to return to their juvenile form, and this we call a 'reversion' in the ontogenetic sense. At the outset it must be pointed out that these phenomena of reversion take place differently even in species of the same genus; they may appear in one species under definite conditions, whilst they will not do so in another, and they are sometimes limited to certain regions of the plant-body, or to a definite stage of development, which once passed, the capacity for 'reversion' is lost. The experimental treatment of this question has been only recently begun [1] and should furnish many valuable results. It has in the first place shown in a number of instances that reversion to a juvenile form chiefly takes place when the conditions of vegetation are unfavourably influenced. We have already seen an example of this in the ferns (page 152). Plants with this capacity behave in some degree like hybrids which have two kinds of 'blood'; the peculiarities of the parents are usually mixed in the hybrid but they may also appear separately, as in the hybrids of many Cacti. Similarly in many malformations of organs—and I mention them simply by way of comparison—we note frequently 'reversions' to the normal form from which they sprang.

Some Bryophyta supply examples showing that the possibility of reversion is associated with a definite developmental stage. The phenomena of germination in the group will be, as I have already said, depicted in the special part of this book, here I only refer to them from the general stand-point. The Marchantieae produce in germination at first a germ-tube, the apex of which develops into a germ-disc out of which the plantlets arise. The primordia of the young plants may be caused to revert to the formation of germ-tubes in Preissia if the intensity of the light be diminished; but only so long as they have not reached the stage at which the permanent vegetative point is formed from which the construction of the higher anatomical differentiation of the plant takes place. The cell-mass which in Funaria hygrometrica arises upon the thread-like protonema as the primordium of a moss-bud can, in like manner, be caused to grow out into protonema-threads [2], but here also only up to a certain age, that namely of the appearance of the three-

[1] Goebel, Über Jugendformen von Pflanzen und deren künstliche Wiederhervorrufung, in Sitzungsber. der k. bayer. Akad. d. Wissensch., xxvi (1896), p. 447.

[2] Goebel, l. c.

sided pyramidal apical cell characteristic of the stem of the moss. It is true that any cells of the shoot-axis or of the leaves may at a later stage form in regeneration protonema-threads, but not so the vegetative point [1]. In one instance, namely Schistostega osmundacea, the apical cell of 'enfeebled' shoots grew out into protonema and therefore it has been assumed that the capacity for this exists in a latent condition in the vegetative point.

The following examples from the higher plants may be cited.

On page 164, I have referred to the band-like primary leaves of aquatic and marsh monocotyledonous plants. It appears that a reversion to the primary leaves may take place in plants whose vegetation is unfavourably influenced (Fig. 104). Plants of Eichhornia azurea, which had wintered as land-plants, produced reversion-shoots with band-like primary leaves [2], and the same occurred in Hydrocleis Humboldti, Potamogeton natans, and others. The genus Sagittaria is specially instructive. The duration of its juvenile form is, as has been said [3], very variable. It is longest in those species which live more as water-plants, shortest in those which are more land-plants. Amongst the latter is Sagittaria cordifolia in which a reversion could not be brought about; the plants when cultivated in water usually died off. On the other hand Sagittaria natans, which lives almost submerged, possesses besides its many band-like submerged leaves only a few floating leaves, whilst in S. cordifolia and others the stalked leaves are not floating leaves. Change of the medium and any other limiting cause produced a reversion to the primary leaves in examples of S. natans which had already developed stalked-leaves.

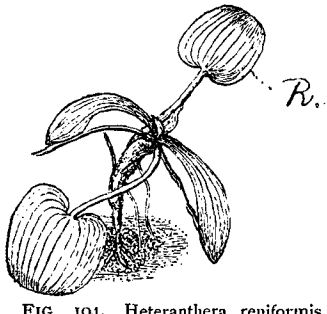

FIG. 104. Heteranthera reniformis. Seedling plant. After producing reniform stalked leaves it again produces band-like leaves as it did at first.

In dicotyledonous plants reversions have been brought about in an analogous way, for example, in Acacia verticillata, a species producing phyllodes. The young plant here, as in other species of Acacia, develops bipinnate foliage-leaves which gradually pass over into phyllodes. In young plants which had already produced a large number of phyllodes and which were enfeebled by cultivation in a dry chamber, reversion-shoots with *foliage-leaves* appeared (Fig. 105). The New Zealand species of Veronica and the myrtaceous Melaleuca micromera which have the xerophilous habit recalling that of the Cupressineae, as described above [4], produce if cultivated in a moist chamber or under unfavourable conditions

[1] See page 47.

[2] See the figure in my 'Pflanzenbiologische Schilderungen,' ii. p. 287.

[3] See p. 164.

[4] See page 167.

the spreading stalked flat primary leaves instead of the adpressed scale-like ones (Fig. 106). In the Cacteae reversion-shoots often appear, but the cause of their appearance has not yet been experimentally investigated[1]. The like holds good for many other plants.

FIG. 105. Acacia verticillata. Young plant which, after reaching a stage in which it formed needle-like 'phyllodes,' has produced on some twigs the bipinnate juvenile form of leaf.

We may say generally that the reversion-shoots appear at definite places and usually near the base of the plant; thus many juvenile shoots appear on the lower part—often covering the stem for several yards—of old plants of Eucalyptus in Italy. The same is the case in Cupressineae, for example, in old plants of Callitris, also in Colletia cruciata[2], and others. From what has been said above we can understand the appearance of the reversion-shoots at the base of plants as, on the one hand, they will be least influenced in this position by the other form of shoot, and, on the other hand, the base can retain from the earliest germination the character of the juvenile form.

FIG. 106. Veronica lycopodioides. The lower part of the shoot shows the entire scale-like adpressed leaves characteristic of the species, in the upper part are the much larger pinnatifid spreading stalked 'reversion-leaves.'

The fact that in *young* plants of Cupressineae injuries by frost, parasites, wounding of the roots, and similar causes induce the development of branches having the juvenile form[3], whilst in normal plants these would have taken that of the adult, conforms with what has just been said. The frequent appearance of reversion-shoots at the base of many plants might find a teleological explanation in the developing shoots having there similar external conditions to those which the seedling finds when it shoots

[1] See what was said about Phyllocactus on page 169.

[2] See Fig. 8 in my 'Pflanzenbiologische Schilderungen,' i.

[3] Beyerinck, in Botan. Zeitung, 1890, p. 539.

out of the ground; but the facts which have been stated show that in the reversion to the juvenile form conformability with purpose cannot be considered as the determining factor. There is a number of plants endowed with this capacity on the advent of definite external conditions, and they react thereto in the same way as does Myriophyllum when it forms winter-buds upon the withdrawal of nutrition[1]—reaction which may have a definite aim but this is not always necessary.

Conclusion of the Development.

An account of the relationships of configuration which follow the juvenile state will be our task in the special part of this book. Here I have only briefly to refer to the question of how far we can speak in plants of adult features. The formation of the organs of propagation, especially of the sexual organs, marks a climax of the development. It causes in many cases the closure of vegetative development, but in others it does not do so. The changes in configuration which precede the formation of the propagative organs, for instance the formation of bracts in the region of the flower, cannot be designated adult features. Where vegetative shoots possess a limited development relationships of correlation are chiefly concerned in it. But even where these are not proved, as for instance in Schistostega, in which the terminal bud of the vegetative shoot which is always unbranched loses after some time its power and dries up, correlations are nevertheless probably effective. In plants which are able to produce organs of propagation frequently time after time the progressive increase of the vegetative framework finally brings about, as has been above stated, the phenomena of 'age' and ultimately death. In Melocactus we find the converse. In it when the plant has attained a certain size there is formed at its summit a 'tuft,' really an inflorescence, which grows persistently for years whilst the vegetative parts neither branch nor probably increase considerably in volume. Here the persistent increase of the flower-bearing region of the plant evidently represents the 'atrium mortis,' for the plant becomes exposed with the increasing size of the tuft always more to injuries, but the vegetative capacity is small and later probably entirely disappears.

[1] Goebel, Pflanzenbiologische Schilderungen, ii. p. 360.

FOURTH SECTION

MALFORMATIONS AND THEIR SIGNIFICANCE IN ORGANOGRAPHY

BRANCH OF THE ASIATIC SOCIETY

MALFORMATIONS AND THEIR SIGNIFICANCE IN ORGANOGRAPHY

INTRODUCTION.

MALFORMATIONS have always been a fertile theme in botanical literature. Not only does every deviation from what we are accustomed to regard as the fixed and therefore *apparently* normal excite our interest[1], but endeavours have been made to obtain through the study of malformations a deeper insight into the homology of organs, and especially of the reproductive organs in the higher plants. We must admit that the investigation of malformations has been of importance in this respect; the transformation of the primordia of stamens into petals, which occurs so commonly in double flowers, led to the first recognition of the 'foliar' nature of the stamen. In recent times through the influence of the theory of descent many malformations, and especially those which have appeared to be *reversions* to primitive relationships of configuration, have been regarded as of special value.

The first question we have to ask is—What do we mean by a malformation? It is impossible to give a sharp definition, for we cannot fix the limit where the normal ceases and the abnormal begins, and the 'normal' itself is a variable quantity. Let us take a concrete example. Anemone Hepatica has usually six perianth-leaves in its flowers, but the number varies. In seventy-five flowers taken at random the following were the numbers of the perianth-leaves: in thirty-five there were six, in twenty-nine there were seven, in ten there were eight, in one there were nine, and in four of the flowers examined there were intermediate formations between perianth-leaves and stamens. The indication here is

[1] It is a frequent experience that people who have not the slightest interest in the normal form of the organs of plants will bring one a malformation because it is 'so interesting.'

that the increase in number of the perianth-leaves has been occasioned by the more or less early transformation of the stamens into petals, and as the number of the stamens is large the function of the staminal apparatus is not disturbed. From such flowers the passage to completely double ones in which *all* the stamens are transformed into petals is a gradual one; but we must designate these double flowers as malformations, because in them a *strong* departure from the normal development has taken place with which is combined a disturbance of function.

Darwin's definition is—'By a monstrosity [malformation] I presume is meant some considerable deviation of structure, generally injurious, or not useful to the species[1].' Moquin-Tandon, the author of one of the best books upon malformations in the Vegetable Kingdom, says[2], 'By an anomaly we mean any extraordinary modification in the formation or the development of organs, irrespectively of any influence upon health.' It is however quite impossible to separate malformations from the appearances of disease. We speak of disease usually when we know the cause of the malformation, for example, the deformity of the buds of the spruce, caused by the insect Chermes Abietis, is an evident malformation, but at the same time it is also a symptom of a disease which has an injurious influence upon the health of the tree only when it is general over the tree. In like manner there can be no doubt that the phyllody of flowers, a favourite domain of teratology, is a symptom of disease; it is a misbirth, the cause of which we do not know in most cases.

What is normal in one plant we must in another regard as abnormal. In Vicia Faba it occasionally happens that the leaves are absent, but their stipules develop strongly, and, as I have shown, do so in consequence of the failure of the leaves. This is certainly a malformation. It is however the normal state in Lathyrus Aphaca. In this plant the foliage-leaves in the upper part of the stem are transformed to tendrils; but we occasionally observe individuals which possess fully formed leaves instead of arrested ones, in, for example, the form known as 'Lathyrus Aphaca unifoliatus.' This feature must certainly be considered a reversion, but if we start from our 'normal' Lathyrus Aphaca of to-day it is a malformation just as are the spikelets which sometimes appear upon the sterile bristle-like twigs of Panicum italicum[3]. In many grasses, especially species of Poa, the flowers are arrested and the axis of the spikelet grows into a vegetative shoot which separates at a later period from the mother-plant; this again is a malformation. But when races have become developed in which this malformation is hereditary, the condition has

[1] Darwin, Origin of Species, Chapter II, first paragraph.

[2] Moquin-Tandon, Éléments de tératologie végétale. Paris, 1841, p. 18.

[3] The occurrence of 'Panicum italicum setis inflorescentiae spiculiferis' has been often described. See A. Braun, in Monatsb. d. Berliner Akad. d. Wissensch. 1875, p. 258.

become normal and serves the purpose of propagation, as is the case in Poa alpina and Poa bulbosa.

These examples will suffice to show that it is impossible to frame a generally applicable definition of the notion of 'malformation.' As I have said, those malformations can be best characterized in which conspicuous changes of the organs have taken place. We find also, if we disregard cases of chorisis, concrescence, and pleiomery, that there is very commonly a change of function, which may go so far as to annul completely the normal function, and with this a change of configuration is associated. Stamens become petals or carpels, or structures which are partly carpels and partly stamens. These transformations have naturally a special interest in relation to the doctrine of metamorphosis.

I.

SIGNIFICANCE OF MALFORMATIONS IN ORGANOGRAPHY.

Whilst we find malformations of any morphological part, the transformations they effect are yet not without rule—a leaf, for example, is never transformed into a shoot or into a root, nor does the converse take place[1]. This is a point of some importance because it shows us that once an organ has been laid down its development is bounded by definite limits[2]. The papilla which develops into a lateral shoot has often the external appearance of the primordium of a leaf; but they must be intrinsically different. Were it otherwise we could not understand why amidst the fundamental disturbances which are observed in many malformations of flowers a transformation of one into the other does not take place. As a matter of fact it was concluded at a very early period from a study of malformations of this kind that petals, stamens, and carpels, are 'leaves,' greatly though they often differ from foliage-leaves in their external configuration. When we know the normal history of development of a plant-organ we can often recognize even in the mature condition the stage of development at which the divergence from the normal in a malformation began, and it is a fundamental principle that a malformation can only be understood through knowledge of the normal development.

Disturbance of the normal development in the sporophylls of the flower, the stamens and carpels, becomes visible in an arrest of the sporangia, the pollen-sacs and ovules, and frequently these do not

[1] Although in the normal formation of organs of Utricularia the limitation between shoot and leaf entirely disappears.

[2] See page 8.

develop. This kind of case has been abundantly used with a view to obtain a decision regarding the 'morphological nature' of the stamen, an endeavour utterly futile as these malformations are obviously disturbances of the normal development provoked by disease. The more the normal development is disturbed the easier is it for the sporangia to be *replaced* by vegetative organs. There is no transformation of the former into the latter, and intermediate stages between the normal and the abnormal conditions do not prove such a transformation, they only show that the disturbance can begin at different stages of development. The morphological significance of the stamen is determined by its developmental history and by comparison with the Pteridophyta, and by these means we learn that the stamen is a sporophyll which like other sporophylls has arisen by the transformation of a primordium of a foliage-leaf[1].

The most completely malformed stamens are those in which there is no trace of formation of the pollen-sacs (sporangia)—a case similar to that of the phyllody of sporophylls of ferns[2]. The stamens then appear either as foliage-leaves or as petals, the latter being the case when the primordium of the stamen before the laying down of the pollen-sacs is affected by the factors which cause the primordium of a foliage-leaf to develop into a petal. In intermediate cases the pollen-sacs appear more or less completely developed, but are usually distorted. Special importance has been attached to those malformations of stamens in which a 'four-winged' leaf is developed, that is to say, a leaf in which two lamellae spring along each side of the length of the midrib. But there is no difficulty in explaining this appearance by reference to the normal history of the stamen. A young stamen, before the appearance of the primordia of the spore-forming tissue is a four-angled body, and in each of the angles the primordium of a sporangium, the archesporium, is differentiated. In phyllody of a stamen each of the four angles grows out as a small leaflet, a phenomenon of growth which is altogether abnormal when compared with the usual condition, but which occasionally is found in a similar way in vegetative leaves. No greater mistake can be made than to consider each leaflet as the product of the transformation of a pollen-sac, for these have not been formed or there is at most a very reduced pollen-forming tissue. What has here taken on the form of a foliage-leaf or part of a foliage-leaf is *not the pollen-sac but a part of the sporophyll*, and we have no more to deal with a reversion than we have when the staminal primordium is transformed into a simple foliage-leaf or into a petal. No useful purpose therefore would be served were

[1] Much of what follows I take from my 'Vergleichende Entwicklungsgeschichte der Pflanzenorgane,' as it is still applicable.

[2] See page 183.

I to recount here the hypotheses which have been built upon these abnormalities, as experience shows that the history of development, and not these hypotheses, has given us the explanation of the relationships of configuration of the stamen. There can be no doubt to the unprejudiced eye that the stamen of an Angiosperm is homologous with that of a Gymnosperm. The theories of malformation however which were framed for the Angiosperms could find no application in the Gymnosperms. But I cannot go further into this matter here. With reference to the phyllody of stamens I have only further to say, that of course the possibility of the transformation of the primordium of a stamen into the lamina of a simple foliage-leaf or of a petal must have existed longer in those plants in which the pollen-mother-cells are only formed at a relatively late stage of development than in those which lay down the archesporium at a relatively early period. In considering then the transformation of the primordia of stamens we have to regard first of all the stage of development of the primordium at the moment when the impulse to the transformation, if such an expression may be allowed, was received, and also the strength of this impulse, for this it is which determines whether we obtain a simple or a four-winged foliage-leaf or petal, or such a leaf with more or less malformed pollen-sacs distorted at their insertion.

In even greater degree than the phyllody of stamens has the phyllody of ovules given rise to morphological hypotheses. The facts are shortly as follows:—

On cultivated plants especially one not infrequently finds flowers altered by disease in which a portion or all of the leaf-organs have the form of foliage-leaves. This is the case, for example, in Aquilegia vulgaris, Reseda odorata, Alliaria officinalis, and others. The cause of this phyllody is mostly unknown. In some cases, as Peyritsch has experimentally shown, it is induced by insects; in others we may assume that the sexual potency has been enfeebled whilst the vegetative has been increased through the nutritive conditions. In flowers which exhibit this phyllody the carpels especially are more or less changed; they are either only enlarged and inflated, or in the place of each carpel a foliage-leaf appears as is so common in Trifolium repens and in other cases, such as the double cherry. When such complete phyllody of the carpels occurs there are usually no ovules; their formation is entirely suppressed. In flowers of Alliaria officinalis, for example, when the most complete phyllody is exhibited we find the sepals, stamens, and carpels, completely transformed into foliage-leaves with buds and shoots in their axils, and the carpels show no trace of ovules. The influence which caused the phyllody of the primordia of the leaves in the flower-bud has here made itself felt even before the ovules were laid down. In less perfect cases of phyllody formations are found in the carpels which are evidently the product of

abnormal development of the ovules, and quite a number of different malformations of the ovule are known. The normal ovule consists, as is well known, of a central body of tissue, the nucellus, which contains the most important part of the ovule, namely, the embryo-sac, and is invested by one or two envelopes, the integuments; and then there is the stalk or funiculus by means of which the ovule is attached to the placenta. The most important question which has to be answered is—how do these several parts behave when phyllody takes place? In every case the phyllody is accompanied *by an arrest of the nucellus*, that is to say, of that part which is characteristic of the ovule, and which enables us to distinguish it from any other body of similar configuration; on the other hand the integuments, and often also the funiculus, experience a vegetative increase and structures like leaflets may proceed from them.

It is now to be noted that the ovules may be subjected to phyllody *at different stages* of their development, and consequently different degrees of phyllody are found. In Fig. 107, *1*, an ovule is represented which

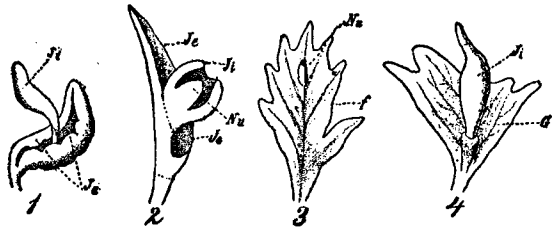

FIG. 107. Phyllody of the ovule. 1–3 Hesperis matronalis. 1. With two integuments; *Ji* inner, *Je* outer. 2. Diagrammatic longitudinal section of a similar stage; *Nu* nucellus. 3. Phyllody of the ovule has set in before the laying down of the outer integument; *Nu* arrested nucellus, *f* 'ovular-leaflet.' 4. Alliaria officinalis. Outer and inner integuments present; G 'funicular lamina.' 1–3 After Celakowsky. 4. After Velenowsky.

has already laid down both its integuments; the inner one (*Ji*) investing the nucellus is only slightly changed, and is seated upon an evident stalk springing from the outer integument which has a scaphoid form as it appears in diagrammatic longitudinal section (Fig. 107, *2*), and shows a more marked phyllody. The phyllody has here seized upon the outer integument because, as happens in by far the larger number of cases, it is laid down later than the inner one, and the displacement of the nucellus with its investing inner integument to the side so that it appears to arise from the surface of the open outer integument, whilst it is really a terminal structure, is not surprising in view of the fact that a similar displacement is frequently seen in normal ovules when the integument is excessively developed and occupies the apex of the ovule. In Fig. 107, *3*, the ovule has become a leaflet which bears the nucellus upon one surface. In this case the outer integument was evidently not laid down at the time when the phyllody began, the inner one was perhaps only just indicated. The funiculus has likewise taken on a leaf-like form, and

the nucellus appears in a lateral position because that portion of the primordium which was immediately below it has grown out into a leaflet. In Fig. 107, *4*, a further case is represented where the outer and inner integuments were both laid down at the moment of the beginning of phyllody, but the lower part of the primordium has become leaf-like and grown out beyond the outer integument. We must also note that frequently the ovule is replaced by a simple leaf if the phyllody has started at a period when neither integument nor nucellus nor archesporium were laid down. This extreme case shows how incorrect it is to regard the phyllody as a reversion: the final result is a simple leaflet, and it would be as absurd to regard this as the most primitive phylogenetic stage of development as to recognize this when the characteristically formed sporiferous leaf-portion of an Aneimia appears as a vegetative leaf if the formation of sporangia is suppressed. The propagative organs, the origin and development of which are involved in both cases, are entirely wanting, and associated with this, and certainly in causal connexion therewith, definite vegetative phenomena appear. That the primordium of an integument becomes a leaflet is no more reason for our requiring to consider that it must have been such a body, than is the occurrence of a cell-group which in phyllody frequently develops into a shoot in the axil of this integument an argument for our considering that it has been a shoot. The only conclusion we can draw from the phyllody is that the integuments are formed out of carpellary substance, in other words, are outgrowths of the carpels, and are the more able to take on a vegetative growth the more the propagative organs—that is, the nucellus—are hindered in their development.

From what we have said it will be evident, without further remark, that we must regard ovules which exhibit phyllody as crippled, diseased, changed, formations. We can only consider it as an error to look upon these kinds of malformations as *reversions*, and wonder that the assertion should have been put forward that a leaflet upon which an arrested nucellus sits, in which form the phyllody of the ovule sometimes appears (see Fig. 107), is the exact homologue of a pinnule of a fern bearing a sporangium or a sorus. As if an arrested papilla in which, so far as we know, not even an embryo-sac is showing had the remotest shade of resemblance to a sporangium! But it would take me too far were I to follow further the erratic paths of doctrines of malformations. It is a much more profitable exercise to go back again to the actual occurrences of malformation and to elucidate the causes which condition the deviation from the normal development; and this question is the more important as its solution can throw light upon the great problem of organic form. The study of malformations is, as the investigations of De Vries show, of special significance in the problems of inheritance and variation.

II.

ETIOLOGY OF MALFORMATIONS[1]

The answer to the question what is the cause of malformations is beset with serious difficulty, inasmuch as we recognize that they can be called forth by *external* influences, whilst examples accumulate to show that malformations are also hereditary and the result of *internal* unknown causes[2]. Examples of the latter class have been longest known.

It is common knowledge that 'double' flowers as well as the remarkable peloria of many plants are transmissible by seeds. Godron[3] found that the peloria in Corydalis solida were transmitted through five generations, and other examples are given by Darwin[4]. Celosia cristata, the well-known cockscomb, behaves in a like manner; I found, in opposition to the statements of other authors, that the transmission of the fasciation is absolute, and that it appears even in plants cultivated in sterile sand, and in the second generation too.

A. All malformations which appear spontaneously, that is to say, which are not caused by external factors, can be at least partly transmitted[5].

The degree to which this takes place varies. For example, only one-third of the seedlings of Acer striatum with variegated leaves inherited the variegation[6]. The investigations of De Vries have in recent times furnished numerous proofs of the transmission by inheritance of malformations. This inheritance is in some cases connected with special external conditions, but in other cases it appears as the normal formation of organs. In the 'viviparous' species of Poa and of other grasses, the formation of flowers and seeds in the spikelets is reduced to a greater or less extent, and is replaced by the growth of the axis of the spikelet into leafy shoots which subsequently fall off. The plants which arise from these shoots repeat the 'malformation,' which is here one of great use to the plant as it provides for propagation in the absence of formation of seed. But this transmission does not take place in all circumstances

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[1] See Goebel, Teratology in modern Botany, in Science Progress, 1896.

[2] It will be shown presently that malformations induced by external causes are often merely the awakening of *latent* predispositions.

[3] Godron, in Mémoires de l'Académie de Stanislaus, 1873.

[4] Darwin, Variation of animals and plants under domestication.

[5] Lowe makes the remarkable statement regarding ferns—'Spores gathered from an abnormal portion of a frond can reproduce this abnormality, whilst spores from a normal portion of the same frond can produce normal plants.' See his 'Fern-growing,' p. 26. Other authors contest this.

[6] Regarding this and other cases see Godron, Des races végétales qui doivent leur origine à une monstruosité. Nancy, 1873 (Extract from the Mémoires de l'Académie de Stanislaus, 1873).

according to Hunger[1], who has observed that when the plants are cultivated in pots these vegetative shoots are suppressed. This however may be the case only when the pot-plants are grown under unfavourable conditions. In viviparous plants of Poa alpina, which I have grown in pots for four years, the vegetative shoots have always appeared. Hunger's observation however is quite in conformity with the facts which have been cited above with regard to reversion to the juvenile form[2]. The formation of flowers must be considered phylogenetically as the older, the buds as having arisen somewhat later; both 'tendencies' are obviously connected with different external conditions, and the plants which produce flowers only are 'reversions' to the original type. Such reversions are also found elsewhere and are of special interest because, like the reversions to the juvenile form, they obviously ensue if the vegetation of the abnormally changed plant is subjected to conditions which are less favourable for it. Thus Lowe states[3] that plants of the varieties of Polypodium vulgare and Scolopendrium vulgare, which are known respectively as 'cambricum' and 'crispum,' and which possess a form of leaf different from the type, if planted in poor soil revert after a few years to the normal form, but do not lose their capacity to produce again the 'malformation[4].' In other examples however this is obviously not the case; they retain even in the most favourable soil their normal form, and the luxuriant nutrition acts not as a factor causing the appearance of the malformation, but purely as one which sets it free[5]. A few examples of the inheritance of malformations are given in the following paragraphs:—

1. Fasciation[6]. De Vries has established the inheritance of fasciation in eight plants. It is true that this is not so absolute that all the individuals show it in the same way, but the fact of inheritance itself is sufficiently evident. As an example Crepis biennis may be cited in which the fasciation appeared so early as in the basal rosette:—

in the	second	generation in	3%
„	third	„	„ 40%
„	fourth	„	„ 30%
„	fifth	„	„ 24%

[1] Hunger, Über einige vivipare Pflanzen und die Erscheinung der Apogamie bei denselben. Dissertation. Rostock, 1887.

[2] See page 171.

[3] Lowe, Fern-growing, p. 30.

[4] The term 'malformation' is rightly applied to them because they are usually sterile. As to the appearance of normal reversion-shoots in abnormal Cacteae see Fig. 5 in my 'Pflanzenbiologische Schilderungen,' i.

[5] With regard to double flowers see Goebel, Beiträge zur Kenntniss gefüllter Blüten, in Pringsh. Jahrb. xvii.

[6] De Vries, Over de erfelijkkeid der fasciatiën, in Botanisk Jaarboek, Dodonaea, vi (1894), with a French résumé; id., Sur les courbes Galtoniennes des monstruosités, in Bulletin scientifique de la France et de la Belgique, xxvii (1895).

Occasionally a generation may be passed over. Thus the seeds from two fasciated capitula of Taraxacum officinale produced in the first year only normal individuals, but in the second year ten fasciated inflorescences appeared upon the same plant, and in subsequent generations as many as 30% of the inflorescences were fasciated. No doubt external influences are of importance; only well-nourished examples with luxuriant growth show fasciation [1], a fact which is quite conformable with what will be stated below.

2. Obligate torsion [2]. By this term A. Braun designated the twisting of stems caused by the concrescence of leaves in a slightly extended spiral line. This occurs as an abnormality in plants in which the leaves are normally whorled; if the position of the leaves becomes spiral and they unite at their base, they form around the stem an imbricate tunic. As the stem elongates it must, so far as possible, unroll the spiral line, and it twists itself in the opposite direction. De Vries was able through the abundance of the material at his disposal to prove the correctness of Braun's explanation of obligate torsions; before his time the isolated cases which were found in nature were all the material available. Once it was proved that obligate torsions could be inherited, numerous examples for investigation were obtainable, and thus the conditions under which the malformation occurs were determined. We have learned therefrom that weak seedlings are not such favourable subjects for obtaining perfect examples of obligate torsions as strong well-nourished plants in which other malformations, such as pleiomery of cotyledons and fasciation, readily appear.

3. Inherited sterility of maize [3]. In a cultivation of maize there appeared completely sterile, altogether unbranched plants. If this habit were inherited we should have a condition quite comparable with that of double-flowered plants which are sterile themselves but are descended from single-flowered plants possessing the 'tendency' to develop double-flowered progeny. An almost sterile plant was selected, one bearing cobs with only very small grains; nineteen per cent. of the progeny was entirely sterile, whilst the progeny of other stronger examples showed only a few cases of sterility.

4. The malformation which occurs in Vitis vinifera and is known as 'Gabler' may be added to the above [4]. In this the tendrils become vegetative shoots and in consequence the formation of flower is entirely suppressed. This kind of malformation occurs occasionally also in the normal vines, but in the true 'Gabler' a permanent race-feature is developed which repeats itself in cuttings. Upon its transmissibility through seed in a manner analogous with the cases previously described nothing is known.

5. An abnormal form of Myosotis alpestris, to which Magnus has directed

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[1] Less well-nourished individuals give also more reversion to the normal form.

[2] De Vries, Monographie der Zwangsdrehungen, in Pringsh. Jahrb. xxiii; Id., Eine Methode Zwangsdrehungen aufzusuchen, in Ber. der deutsch. botan. Gesellsch. xii.

[3] De Vries, Steriele Maïs als erfelijk ras, in Bot. Jaarboek, Dodonaea, ii (1890); Id., Over sterile Maïs-planten, ibid. i (1889).

[4] E. Rathay, Über die in Nieder-Österreich als 'Gabler' oder 'Zweiwipfler' bekannten Reben. Klosterneuberg, 1883.

attention, with pleiomerous, partly proliferous flowers has been proved to be heritable [1].

In conclusion I may mention the research of Heinricher [2], who found that the second staminal whorl which is normally absent in Iris could be handed down as a hereditary character. The members of this whorl are indeed very variable; sometimes they appear as arrested stamens, sometimes as completely formed ones; they may be staminodia with or without pollen-sacs, or they are style-like structures. A perfect fixation, that is to say, the breeding of a stock with only atavistic flowers, has not yet been attained; but it is of special interest that flowers have appeared in which the inner perianth was constructed like the outer, and that a flower-form has also been found which diverged far from the ordinary one and may perhaps be considered as an advance in development of the reverted type.

B. There is another series of cases—those in which malformations have been experimentally evoked. Here we leave out of consideration the phenomena as they are determined by want of light and like agencies.

The lower plants, especially the Fungi, are particularly favourable for this kind of investigation, and a few examples may be cited:—

Dematium pullulans, which consists commonly of ordinary hyphae or of yeast-like sprouts, if it be cultivated for a long time in a temperature of 30–31° C. produces cell-masses by the division of its cells in every direction of space, and the individual cells in these masses may at a normal room-temperature again sprout out in a yeast-like manner [3]. The interesting malformations which Raciborski has recently produced in Basidiobolus ranarum are in a certain degree analogous [4]. This plant normally consists of uninucleate cylindric cells arranged in a thread-like series, and it is easily cultivated in a nutritive solution. If the concentration of the solution be gradually increased the cells always become shorter and approach the spherical form and their dividing walls become more oblique; this never happens in normal growth. If now the culture is brought into a 10% glycerine solution at a higher temperature, say 30° C., plurinucleate giant-cells with a diameter of 60 μ frequently develop and between some of the nuclei delicate cell-walls appear. All the cells do not react alike. It is evident that here a profound disturbance of the growth has taken place; the giant-cells have no power of development; they die off. Other abnormalities need not here be mentioned,

[1] Magnus, Teratologische Mitteilungen, in Verh. d. bot. Vereins. d. Provinz. Brandenburg, 1882.

[2] Heinricher, Versuche über die Vererbung der Rückschlagserscheinungen der Pflanzen, in Pringsh. Jahrb. xxiv.

[3] Schostakowitsch, Über die Bedingungen der Konidienbildung bei Russthaupilzen, in Flora, lxxxi (Erg.-Bd. z. Jahrg. 1895), p. 376.

[4] Raciborski, Über den Einfluss äusserer Bedingungen auf die Wachstumsweise des Basidiobolus ranarum, in Flora, lxxxii (1896), p. 107.

I may only say further that if Basidiobolus be cultivated in a 1% solution of ammonium-sulphate or a 1% solution of ammonium-chloride it may be induced to form a 'palmella-stage' such as is known in no other fungus—it breaks up into spherical cells with thick walls, and these are then set free from the old cell-envelope. In this case the arrest of the development is apparently not so far-reaching as it is when the giant-cells are produced.

We meet with similar phenomena in some Algae. In them the nature of the nutrient solution, especially its concentration, will call forth malformations although these are not so extensive as they are in Basidiobolus. Thus Chodat and Huber[1] found that the formation of daughter-colonies was suppressed in Pediastrum Boryanum, when it was grown in concentrated nutrient solutions, and the cells sometimes became large 'hypnocysts.' Richter[2] produced similar abnormalities by cultivating other freshwater algae in salt solutions.

Passing now to the Spermaphyta, I must in the first instance quote the words with which Peyritsch, one of the most fertile investigators in the domain of the causes of malformations, introduces his treatise upon the etiology of the formation of peloria[3]: 'In the investigation of the etiology of peloria, and generally of deviations in construction from the normal, there are two factors which must not be lost sight of; one is the immediate *determining* cause, which in many cases may be an external agent, and the other is an internal factor, namely, the *predisposition* to the development of the anomaly. It is easy to convince oneself that all the individuals of the same species do not react in the same way towards the same external injurious agencies, and that their reaction also varies at different times. The capacity to change, to appear in abnormal forms, to become diseased, does not exist in all of them in the same way.' This is a conclusion to which the researches of de Vries above referred to also lead. It is not however to be regarded as applicable solely to cases of malformations, it holds for the operation of all external factors upon relationships of configuration, and in malformations we have merely the evidence of predispositions which do not normally show themselves. Whether we are to consider peloria as malformations or as reversions is of no moment for our question here. No doubt these wonderful forms of flower exhibit a more primitive type than the dorsiventral flowers which are the normal ones in the plants in which they occur.

With regard to the etiology of peloria, it is known that if terminal flowers are produced upon shoots which otherwise have only dorsiven-

[1] Chodat et Huber, Recherches expérimentales sur le Pediastrum Boryanum, in Bull. de la société bot. Suisse, 1895.

[2] Richter, Über die Anpassung der Süsswasseralgen an Kochsalzlösung, in Flora, lxxviii (1892), p. 4.

[3] Peyritsch, in Denkschriften der Wiener Akad. d. Wissensch. xxxviii (1878).

tral flowers, such terminal flowers are almost without exception peloria; but lateral flowers may also develop as peloria. The influence of position upon the dorsiventral or radial construction is here unmistakable, although the attempt to prove this by experiment has been scarcely successful. Thus Hoffmann[1] endeavoured to arrive at the formation of peloria by placing in a vertical position the flower-buds of Achimenes grandiflora, Salvia Horminum, Gloxinia speciosa, and other plants; but the negative outcome of such an experiment is of course evident from the first, because at the time when one can operate upon flower-buds which are laid down dorsiventrally their construction has already reached such a stage that no essential change is to be expected. Numerous as are Hoffmann's experimental cultures they can scarcely be cited as of critical value. Peyritsch has endeavoured to discover the immediate cause of the formation of peloria in another way, as he states in his paper cited above. Starting from observations made upon plants in their natural habitats he asked himself whether the formation of peloria could not be caused by a change in the conditions of life, and experiments with Galeobdolon luteum and Lamium maculatum proved that this is the case. It is true that the experiments leave many important questions still unanswered, nevertheless I mention their results because an extended repetition of them is most desirable.

The plants of Galeobdolon luteum grew in their natural habitat under the shade of other plants. If now the shading was removed, for instance by cutting down the trees in the vicinity, peloria frequently appeared, and along with them other anomalous conditions of the flowers. The conclusion was then natural that the increase of the intensity of light (or transpiration) was the cause of the malformations of the flowers, and the experiment obviously supported the correctness of the view that a change of the conditions of life induced variations in plants. The plants were then placed in localities with stronger insolation, but unfortunately no control experiment was made such as the division of the stock and the placing of a portion of the plants in normal shady places. Some of the plants developed no flowers at all; others changed their time of flowering and the flowers appeared upon shoots which normally possessed no flowers; *three individuals produced terminal peloria;* two remained normal in the main, but in one of them there appeared a flower abnormal in the numerical relation of the flower-leaves. In the following year the abnormal phenomena were less marked, the plants appeared to be getting accustomed to the new conditions of life, and that the formation of flowers was generally lessened may be explained by the unfavourable influence exerted upon the whole growth. In Lamium maculatum similar anomalies appeared, but, as in Galeobdolon, they never

[1] Hoffmann, in Botan. Zeitung, 1875, p. 625.

extended over the whole plant. In the vegetative region abnormalities were occasionally noticed, but all plants did not react in like manner.

We may here merely direct attention to the long known fact, which has been mentioned above, that in a number of plants, for instance Digitalis purpurea, the formation of peloria is inherited through seed; Peyritsch has proved it in Leonurus Cardiaca. In Galeobdolon and Lamium however the inclination to the formation of peloria, which we must here assume to be latent only, is expressed if special external conditions give the stimulus.

We have also to bear in mind the fact that we can produce *fasciation* artificially by causing the 'sap' to flow rapidly and with great intensity into a lateral bud which otherwise would only obtain a small part of it. This is why fasciation is specially common in stool-shoots and in sucker-shoots. In annual plants also like Phaseolus multiflorus[1], and Vicia Faba, if one cuts off the chief axis above the cotyledons the axillary shoots instead of developing normally are then frequently fasciated. On this kind of shoot there appear also not infrequently 'double leaves[2].' This happens particularly in plants with decussating leaf-pairs like species of Weigelia and Lonicera. The phyllotaxy changes, and instead of dimerous whorls trimerous whorls appear. At the limit where these different arrangements meet we often find transition-stages from a more or less deeply bifid leaf to two separate leaves standing close to one another; such leaves however also appear although the phyllotaxy is unchanged. They evidently arise because under the influence of the increased nutrition the shoot forms three instead of two primordia of leaves, and of the three two lie close together; if the plastic material sufficient for the development of two leaves flows to these then they remain separate and form two leaves, if this is not the case then one bifid leaf is developed[3]. Such malformations are found on shoots which develop after lopping of the chief axis, but I have also seen them on uninjured individuals of Weigelia which were richly nourished.

Luxuriant shoots often exhibit other marked variations in the form of their leaves, apart altogether from mere size, and these, although one cannot perhaps speak of them as malformations, may fitly find some notice here. In Symphoricarpus racemosus the leaves are commonly simple and entire, but they are pinnatifid on luxuriant 'renovation shoots.'

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[1] Sachs was the first who proved this in this species.

[2] See J. Klein, Über Bildungsabweichungen an Blättern, in Pringsh. Jahrb. xxiv, 425; Celakowsky, Über Doppelblätter bei Lonicera Periclymenum und deren Bedeutung, in Pringsh. Jahrb. xxvi, 1—the literature is cited here.

[3] Many authors interpret this as a more or less deep splitting of a leaf-primordium. I do not think this view is correct. I regard it as quite similar to what is easily observed in the Cacteae, namely, that increased nutrition leads to an increase in the number of the orthostichies. It would take me too far to give an explanation in detail here.

Upon the sucker-shoots of Sambucus nigra[1] the stipules, which are usually arrested, are well-developed and the leaf-lamina is more divided than is usual. Other examples are common. Similarly I have been able by removing the chief shoots to cause the simple primary leaves on the basal lateral shoots of Vicia Faba to grow out into foliage-leaves, or to form intermediate formations between foliage-leaves and primary leaves which any teratologist would recognize as true malformations (see Fig. 94); and A. Mann was able in like manner to bring about in a series of investigations, undertaken at my instigation, the partial development into leaves of the tendrils of Pisum sativum. Sachs was able to evoke a very interesting malformation in the roots of Cucurbita by removing all the vegetative points of the shoots: the primordia of the roots lying to right and left in the tissue of the stem beside the stalk of each foliage-leaf grew out into shortly stalked tubers about the size of a hazel-nut or walnut; on them the root-cap disappeared and the vegetative point was not recognizable, and the axile bundle-strand was broken up into a circle of bundles separated from one another by a tissue containing chlorophyll; there was thus produced a differentiation of tissue like that of a shoot-axis[2].

A change, though not so far-reaching in character, is that which arises from less favourable relations of nutrition. Juncus bufonius has the normal trimerous flowers of other species of Juncus. Buchenau[3] found dimerous flowers in dwarfed examples grown upon sterile soil, whilst Juncus capitatus grown under similar conditions exhibited no change in the numerical relationships of its flower. In Juncus bufonius also this variation does not always take place; when it occurs there is always an evident influence inducing it. With regard too to the distribution of the sexes in normal dioecious plants like the willows, the effect of external conditions sometimes makes itself felt, and pistillate flowers may appear on staminate plants or there may be hermaphrodite flowers, and the converse is the case. Thus Hampe[4] observed in Salix repens that those twigs which sprang from branches growing under water and reached the surface bore female flowers, whilst those which came into flower after the drying up of the water were male. Any disturbance of the normal conditions of vegetation will in general favour expression of the latent possibility that exists to produce female flowers on male plants. Thus Haacke[5] describes the transition from female flowers into male ones in a much mutilated female plant of Salix Caprea. In all these cases we have to deal with definite material influences, and we must also assume

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[1] See Fritsch, in Österr. botan. Zeitschrift, 1889, Nr. 6.

[2] Sachs, Gesammelte Abhandlungen über Pflanzenphysiologie, ii. p. 1172.

[3] Buchenau, Kleinere Beiträge zur Naturgeschichte der Juncaceen, in Abhandl. d. naturw. Vereins zu Bremen, ii.

[4] Hampe, in Linnaea, xv. p. 377.

[5] Haacke, in Biolog. Centralblatt, 1896, p. 817.

that these are operative when the cause of the malformations is either an animal or a parasitic fungus.

With regard to the changes brought about in the form of a host-plant by an attack of parasitic fungi it is scarcely necessary to recall here the remarkably varying degree in which they appear; they are often so slight that there is scarcely anything to be seen of them on the outside. We should naturally expect a much stronger effect where the parasite influences *embryonal* tissue, as happens especially at the vegetative points. The outgrowths which appear on many shoot-axes and leaves must remain unnoticed here[1], as well as all the numerous cases of abortion. I shall only notice some examples in which the whole form of an organ is affected by the parasite in such a way as to be designated a malformation. We have in these cases to do with not merely the transformation of an organ, but with the development of organs which might otherwise remain latent, and also with the new formation of organs.

Upon the branches of the silver fir, as well as upon other species of fir, 'witches' brooms' frequently appear, that is to say, negatively geotropic shoots bearing needle-leaves which are annual in duration in contradistinction to those of the normal shoots, and are also distinguished from the normal leaves by structure and form. These abnormal shoots are caused by the penetration into a bud of the mycelium of Aecidium elatinum. They are always sterile, as are the shoots of species of Euphorbia when they are attacked by Uromyces pisi, and take on in consequence a habit strikingly different from the normal. Species of Exoascus may also cause abnormalities in the branch-system of the cherry, birch, and other trees, which have, too, been designated 'witches' brooms[2].'

If Peronospora violacea attacks the flowers of Knautia arvensis there is often induced a transformation of the primordia of the stamens into violet petals, that is to say, a 'doubling' of the flower[3]; in other cases there may be only an arrest in the development of the staminal leaf or the appearance of a petal-like wing in place of a pollen-sac. Giard found that in Saponaria officinalis in like manner flowers which were attacked by Ustilago antherarum had their stamens sometimes transformed into petals, a transformation which, as we shall see, frequently happens on account of the attack of animals.

These are examples of a divergence in their development experienced by the primordia of organs which would otherwise unfold in a different

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[1] The mycological literature should be consulted for these; see particularly De Bary, Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria, and the comprehensive account by von Tubeuf in his 'Diseases of Plants induced by Cryptogamic Parasites.'

[2] See the many figures in Tubeuf's book cited in the preceding note.

[3] De Bary, Comparative Morphology and Biology of the Fungi, p. 368; Molliard, Cécidies florales, in Annales des Scienc. Nat., sér. 8, i.

way. But organs which are normally arrested may be caused to develop further by the attack of a fungus. Lychnis vespertina[1] is a common dioecious plant, but it sometimes occurs with apparently hermaphrodite flowers. In all cases which have been carefully investigated this latter condition is the result of an attack upon the female flower by Ustilago antherarum bringing about the full development of the primordia of the stamens which would otherwise be arrested at an early stage; in the anthers however the spores of Ustilago are found instead of pollen-grains, and the female sexual apparatus is in great part aborted.

An example of the *new formation* of organs at places on which they would not otherwise appear is known. We have such in the 'witches' brooms' which are formed upon the leaves of Pteris quadriaurita in consequence of the attack of the fungus Taphrina Laurencia[2]. These are adventitious shoots with malformed leaves, although normal adventitious shoots never appear upon the leaves of this plant; but in other species the appearance of leaf-born shoots serving the purpose of vegetative propagation is normal. The leaves of these adventitious shoots differ in form and structure from the ordinary leaves of Pteris; the form may be seen in Fig. 108; as to the structure, I need only say that it is much more simple than that of the normal leaves, the leaf-tissue is but slightly differentiated, the epidermis possesses no stomata, and the leaves, teleologically considered, are evidently destined here, as they are in the tissue-growths of other 'fungus-galls,' to draw from the plant-body plastic material which the fungus then converts to the formation of its own spores. These deformed leaves are nevertheless merely transformations or arrestments of ordinary primordia of leaves, as is shown in the fact that they are laid down and grow like normal leaves, and that there may appear, seldom it is true, amongst them a *normal* leaf of Pteris; this comes about because the fungus-hypha has not pierced the primordium of the leaf. The process is then evidently this—in consequence of the attack of the parasitic fungus the leaf-tissue is caused to form an adventitious shoot which otherwise would not develop here, and the fungus changes by its attack the primordium of the leaf. The first effect recalls at once the formation of galls on Selaginella pentagona, about which we shall say something presently[3].

Buchenau[4] found in plants of Luzula flavescens and Luzula Forsteri which were attacked by a brand fungus that the flowers were replaced

[1] Magnin, Recherches sur le polymorphisme floral, la sexualité et l'hermaphroditisme parasitaire du Lychnis vespertina. Lyon, 1889. For analogous cases in other plants, see Magnin et Giard in Bull. scientif. de la France et de la Belgique, xx (1889), p. 150.

[2] See Giesenhagen, Über Hexenbesen an tropischen Farnen, in Flora, Erg.-Bd. 1892, p. 130.

[3] See page 197. With regard to the fungus-galls of Aspidium aristatum, see Giesenhagen l. c.

[4] Buchenau, in Abhandl. d. naturw. Vereins zu Bremen, ii.

by dense tufts of bracts, and this is a natural step towards the phenomena of phyllody brought about by the attack of insects.

The work of J. Peyritsch[1] upon the artificial production of double flowers and other malformations is of great interest, and it is unfortunate that owing to the death of the author we have been deprived of the detailed exposition of the results of his experiments which he had promised, and only possess the two short communications cited in the note.

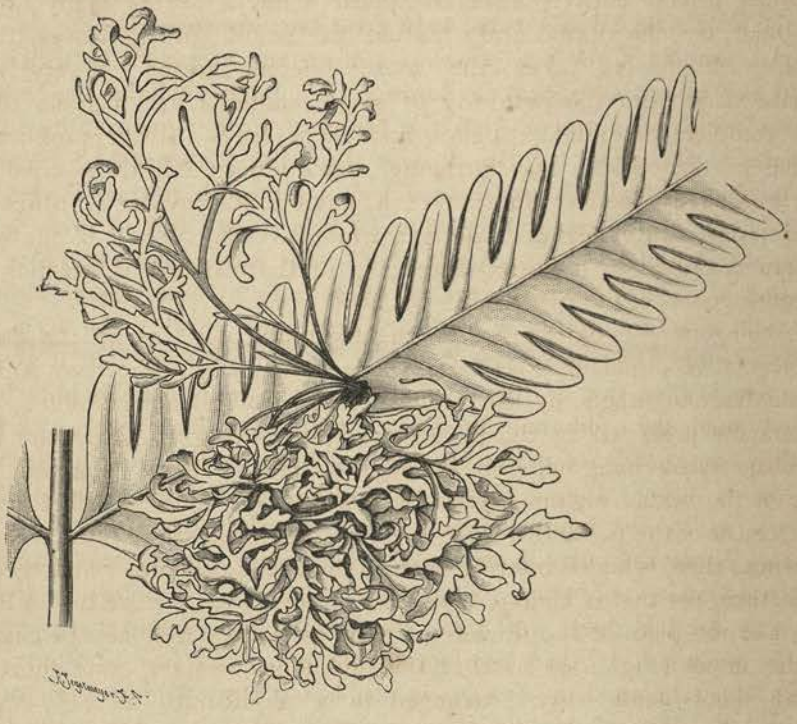

FIG. 108. Pteris quadriaurita. 'Witches' broom' upon a leaf-pinna. Its leaves differ in form from the normal ones of the fern. The malformation is induced by the attack of the parasitic fungus Taphrina Laurencia. After Giesenhagen.

In the second of these Peyritsch has shown that in species of Arabis phyllody may be produced by artificially infecting them with aphides provided that the flower-buds are not in too forward a stage of development. A disturbance of the formation of the sexual organs is associated with the phyllody, the pollen especially being rudimentary and obviously functionless.

Far-reaching malformations have been produced in Valerianeae and

[1] J. Peyritsch, Über künstliche Erzeugung von gefüllten Blüten und anderen Bildungsabweichungen, in Sitzungsber. der Wiener Akad. der Wissensch., xcvii (1888); Id., Zur Äthiologie der Chloranthien einiger Arabis-Arten, in Pringsh. Jahrb. xiii.

Cruciferae through infection with Phytoptus; they have the form partly of abnormally shaped leaves, partly of varying states of doubling and prolification of the flower. The modifications of the leaves are in general of such a kind that fringes like the teeth of a comb are developed upon lobes which usually project over the leaf-edge. In Centranthus Calcitrapa the condition called by Masters[1] 'enation from foliar organs' often appears. In the inflorescence of Cruciferae the bracts which are usually entirely aborted appear below a few or many flowers, and take on the form and texture of small foliage-leaves. The doubling of flowers takes the most different forms. Every intermediate stage from the petalody of single stamens and carpels to the most complete doubling appears, and there may also be prolification, tripling of the corolla, calycanthemy, and so on. All these conditions were evoked by the introduction of a parasite, a Phytoptus, which was found in degenerate buds of Valeriana tripteris. The degree of the transformations caused by it varied according to the amount of infection and the sensitiveness of the plant.

Analogous phenomena are frequently produced both in the flowers and vegetative organs of species of Juncus, such as lamprocarpus, supinus, acuminatus, and others, by the prick of an insect, Livia juncorum[2]. The appearances produced in the flowers vary according to the moment at which the transforming influence of the insect affects them. Commonly an arrest of the sexual organs occurs, but besides this there is sometimes an enlargement of the perianth-leaves to quite three times their normal length, sometimes there is bud-formation in the axils of the perianth-leaves through which their position is changed, and in extreme cases a large tuft of leaves may take the place of the flower. Vegetative shoots may also be changed by the insect (Fig. 109) so that the internodes remain quite short and lateral shoots with leaves arranged in a phyllotaxy of $\frac{1}{2}$–$\frac{1}{3}$ develop in the axils of almost all the leaves[3]. The changes to which the leaves themselves are subjected are however specially peculiar; the vagina is greatly enlarged whilst the lamina remains small or may be entirely aborted[4], in other words, *the insect brings about here the same changes which take place otherwise in the normal 'leaf-metamorphosis' when a cataphyll or a hypsophyll arises from the primordium of a foliage-leaf.* The advantage to the insect is that the soft tissue of the leaf-sheath attacked at the period of elongation furnishes it more easily with food.

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[1] Masters, Vegetable Teratology, p. 445.

[2] See Buchenau, in Abhandl. d. naturw. Vereins zu Bremen, ii. p. 390. This is one of the commonest of malformations; in the vicinity of Munich abundant examples may be found.

[3] This is not however regular and there is much torsion and displacement.

[4] These malformations ought to be studied by those botanists who in spite of the history of development and other evidence will persist in regarding the leaves of the rush as shoots.

Turning again to the investigations of Peyritsch[1]—two points seem to me to be of special significance,—

1. In the formation of galls a *material* influence of the parasite is the cause of the malformation.

2. *In the malformations no formation of new organs usually occurs but only a derangement of the organs.*

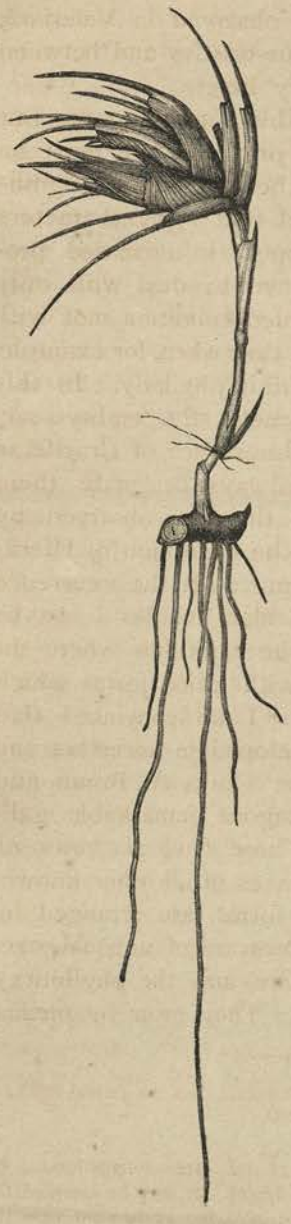

FIG 109. Juncus lamprocarpus. Shoot transformed by the attack of the insect, Livia Juncorum. The vagina of the leaves is greatly developed, the lamina is reduced.

The cases already described of the attack of fungi show us however that in malformations new relationships of configuration may also appear; and with reference to the 'derangement' of organs I may remark that when a flower exhibits phyllody the foliage-leaves which replace the petals, stamens and carpels, have the ordinary form of the foliage-leaves of the species; even to the characteristic 'tentacles' in such plants as species of Drosera. Phyllody is not always complete, and then naturally the form of the leaves is more simple, but the extreme cases are always the clearest. Further, when in the doubling of flowers new petals appear these have usually the form of the ordinary petals; the malformation consists in an abnormal transformation and in a mixing up in some degree of the different organs. But just as in the formation of galls new tissue-elements which are not found otherwise in the plant do not commonly appear, so in these malformations nothing new of a morphological character arises[2]. What is new is only the com-

[1] With reference to other form-changes induced by animals see the summary by Frank in his 'Pflanzenkrankheiten,' Part iii.

[2] It is open to question whether this is always the case. It might be otherwise. Herbst, in the 'Biologisches Centralblatt' for 1895, points to the fact recorded by Solms-Laubach that in the fungus-galls produced upon Polygonum chinense by Ustilago Treubii the tissue of the host-plant furnishes capillitium-like cells which co-operate in the scattering of the spores by increasing, as Solms says, the difficulty of wetting the free-lying cells. Still what really takes place here is that cells of the host-plant are stimulated to elongation by the growth of the fungus and these are, like the tissue of other galls, of use to the parasite, not to the host (see Solms in Ann. Jard. Bot. de Buitenzorg, vi. p. 79). Moreover there are cell-forms which are non-existent if the development is undisturbed, for instance, the hair-formations of 'Erineum-galls'; and these hair-formations, which are induced by the attack

bination of the possibilities of the plant, the peculiarities which are combined remain the same, like the pieces which furnish the changing pictures in a kaleidoscope. Formations intermediate between two organs arise in this way very often, and Peyritsch has observed in Valeriana intermediate formations between bracts and pappus-bristles and between bracts and petals taking the place of the ordinary bracts.

Seeing then that in these malformations nothing new appears, but there is only a different combination of existing primordia, we must be on our guard against assigning to malformations the phylogenetic significance which is often assigned to them[1]. Granted that many characters which exist in the plant as *latent primordia*[2] appear in increased proportion when malformations develop, yet we have to deal with only the *unfolding* of existences in a somewhat enfeebled condition, not with a change of the whole formation of organs as is the case when, for example, the ovules appear as leaflets in flowers which exhibit phyllody. In this latter case the characteristic of the ovule, namely, the embryo-sac, has disappeared. But when the bracts of an inflorescence of Cruciferae develop one may upon comparative grounds always designate them a reversion. In this way one should interpret the facts observed by Treub[3] and others, that in the gall-formations of the capitulum of Hieracium umbellatum every transition from normal pappus up to the occurrence of five separate green leaves provided with vascular bundles is to be found between the involucre and the middle of the capitulum where the gall-apple sits. It is however only comparison with allied forms which can lead us to an interpretation of this kind, for I am convinced that there are latent primordia which were never developed in ancestors and which therefore have no phylogenetic significance. Thus A. Braun and Strasburger[4] have observed in Selaginella pentagona remarkable gall-formations which are externally like bulbils. These have six rows of leaves which are all constructed alike, whilst the leaves in all other known species of Selaginella, except a few isophyllous forms, are arranged in obliquely crossing pairs and in each pair the leaves are of unequal size. These gall-shoots are inhabited by dipterous larvae, and the phyllotaxy they exhibit is seen nowhere else in Selaginella. They grow by means

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of mites, are serviceable to the parasite and diverge altogether in structure from the normal hairs of the plants on which they occur.

[1] See the first paragraph of this Section.

[2] Neottia nidus-avis, the well-known saprophytic orchid, has no green foliage-leaves, but occasionally one may appear. Its primordium must have been latent. It may be assumed that there is here an inheritance from ancestors furnished with foliage-leaves, but at the same time it is allowable to ask—is there any reason why there should not be latent primordia which are *not* vestiges of an earlier development?

[3] Treub, Notice sur l'aigrette des Composées, in Arch. Néerl. viii.

[4] Strasburger, Die Bulbillen und Pseudobulbillen der Selaginella, in Botan. Zeitung, 1873, p. 105.

of a three-sided pyramidal apical cell. The first stages of the development are unfortunately unknown, but they probably arise as growths on juvenile shoots in consequence of the stimulus induced by the larva. We have no ground for assuming that the ancestors of this Selaginella have at any time had shoots with six rows of leaves, or that the ancestors of Pteris quadriaurita developed adventitious shoots upon their leaves[1]; we must rather believe that these malformations are new formations whose nature depends on the one hand upon the protoplasm of the plant, and on the other upon the stimulus acting upon it. Lower plants, especially fungi, appear to be more plastic in regard to the production of malformations than are the higher plants in which, as we have seen, only a derangement of the formation of organs occurs.

What has just been said regarding the malformations caused by insects leads me to cast a glance upon the more recent investigations into the occurrence of galls. These wonderful structures have from an early time attracted attention. We observe in them the formation of a new structure in consequence of a stimulus exerted by an insect, and it serves in an exceedingly effective manner for habitation, nourishment, and protection to the developing insect. Whence proceeds this stimulus? According to Lacaze-Duthier[2], with whom Darwin and Hofmeister agree, a poison which is introduced by the ovipositor of the insect when it lays its eggs is the cause of the formation of the gall. Of course a susceptibility to the stimulus exercised by the insect must exist in the plant, for we find that the 'virus' of Cynips Rosae, for example, has no effect upon the oak although this tree produces so many different galls. The theory of Lacaze-Duthier has been however proved untenable in many cases through the famed entomological investigations of Adler. Beyerinck[3] too has enriched our knowledge of the formation of galls, especially from the botanical side.

It has been shown in the case of Cynips-galls that the stimulus which causes the formation of the gall is not given by the wasp which lays the eggs but by the larva; and the larva exercises its influence while still completely enclosed in the egg. We can hardly think of this as occurring in any other way than by the excretion from the larva of a soluble substance which penetrates into the tissues of the plant, for the larva is often separated from the tissue developing into a gall; it may even be divided from this in some cases by dead tissues, and yet the origin of the gall is not retarded. This shows that we have not to do with the conduction of a stimulus through the living protoplasm of the host-plant. Inasmuch as the influence proceeds from the larva and is a slow one, the

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[1] See page 193.

[2] Lacaze-Duthier, Recherches pour servir à l'histoire des Galles, in Ann. d. Sciences Nat., 1853.

[3] Beyerinck, Beobachtungen über die ersten Entwicklungsphasen einiger Cynipiden-Gallen. Amsterdam, 1882.

development of the gall can be brought to a stop by the death of the larva. We know that wound-stimulus does not play the chief part in the formation of galls, because in many cases the eggs are fixed on the *surface* of young organs of plants, and are then invested from the sides by the tissue which lies round about them. The larval chamber, which is always lined with nutritive tissue for the larva, arises through an arrest of growth at the position of the young gall-tissue which is immediately in contact with the larva.

Adler discovered, and Beyerinck has confirmed his statement, that the different forms of one and the same gall-wasp produce different forms of galls upon one and the same host-plant—the oak; and this is of special importance in relation to any theory of the formation of galls. The females of Dryophanta folii, for example, leave their galls upon the oak-leaves in November or December; they seek out a bud, a 'sleeping eye,' lay an egg upon its vegetative point, and thereby produce a small violet-coloured bud-gall which, before its true connexion was discovered, was ascribed to a gall-wasp termed Spathegaster Taschenbergi. The males and females of this species leave their habitations in May, the fertile females prick the ribs of young oak-leaves and thereby occasion the formation of the leaf-galls from which we started. The two kinds of galls are quite different both in form and anatomical structure. The question then is—is the material, causing the formation of the gall, which is excreted from the eggs originating parthenogenetically, different from that exuding from the fertilized eggs, or, if the material be the same, is its reaction on a vegetative point different from that which it exerts upon a leaf? The answer to this question I consider of more importance for morphology than the pursuit after apical cells and other questions of detail upon which so much time has been expended.

The galls are adapted in a remarkable degree to the needs of the larvae, as has been already stated, and it is of special interest to observe that the protection of the developing insect in the gall is effected partly mechanically, partly chemically—especially by a copious formation of tannin—but the protection is in no degree absolute, as the numerous inhabitants of the galls tell.

How remarkable are the formations which arise in this way is shown in the galls of the microlepidopterous Cecidotes Eremita which are found on the twigs of shrubs of the genus Duvaua[1] in Argentina. The spherical to oval gall arises from the *cambium* of the branch; it possesses a cambial meristem lying parallel with its surface from which is developed in a radial direction inwards a nourishing tissue of thin-walled cells rich in protoplasm for the caterpillar, whilst towards the outside

[1] Hieronymus, in Jahresber. der Schlesischen Gesellschaft für Vaterland-Cultur, 1884, p. 272.

sclerenchyma and vascular bundles are produced. There is a lid to the gall, which, produced without any special aid of the insect, enables it at a later period to leave the gall-chamber which served for its protection.

In another gall protection is provided by the development of *roots* in consequence of the stimulus of the larva, and these grow over the larval chamber, stick to one another and make a dense living mantle. This is what is found in the galls of Cecidomyia Poae upon Poa nemoralis[1]. The roots arise here at places where under normal conditions they would never appear. The gall-forming stimulus passes in this case from the larva which is firmly fastened to the surface of a still growing internode; cushion-like swellings are first of all formed right and left of, but at some distance from, the larva, and from these the roots then take their origin, and these roots can be caused to develop further as normal roots by using a gall as a cutting. The behaviour of Nematus Capreae[2] shows however that the gall does not originate in every case through the exercise of a stimulus of the larva. In this case, as Adler found, the facts agree with the old theory of Lacaze-Duthier; the development of the gall is dependent upon the substance introduced with the egg into the young leaf from the poison-bag; the formation of the gall is evoked by any wounding effected by the saw of the insect even though no egg is deposited, and the artificial destruction of the egg does not here arrest the gall-formation, the development of the egg only affects the size of the gall.

In concluding this short reference to recent investigations into the formation of galls I would only emphasize these two points—

1. In general no tissue-elements appear in the anatomical structure of the gall which do not exist elsewhere in the plant under other conditions;

2. All the more highly differentiated galls are produced out of juvenile tissues still capable of development which are caused to develop in an abnormal way by the influence of a gall-insect; the more complex in structure a gall is, the earlier must the influence producing it be exerted upon the plant-tissues.

III.

SIGNIFICANCE OF MALFORMATIONS IN THE THEORY OF FORMATION OF ORGANS.

I have already pointed out some general reflections which arise from the study of malformations, and I will now shortly state to what theoretical considerations they have led.

We must in the first instance refer to Sachs' idea of 'material and

[1] Beyerinck, in Botan. Zeitung, 1885, p. 305.

[2] Beyerinck, Über das Cecidium von Nematus Capreae auf Salix amygdalina, in Botan. Zeitung, 1888.

form[1]' which has special bearings upon malformation. Sachs proceeds from the proposition that the differences in *form* of the organs of plants are based on their *material* differences, and that the changes of organic form are in touch with changes in the processes of nutrition. The substances which cause the formation of a foliage-leaf are then different from those required for the formation of an ovule, of a root, and so forth. If this be the case, then the so-called 'morphological processes' are causal, just as this is true of, for example, the morphology of a crystal, and we can picture to ourselves how it comes about that in malformation one organ so frequently appears in place of another organ, or that the relationships of form of the two kinds of organs are mixed up together in the most different ways, even as the peculiarities of two species are combined in their hybrid; such intermediate formations are the result of the wandering into the primordium of one organ of the material which belongs to the formation of another.

The malformations caused by insects show us that the formation of organs is changed through material influences, although of course the changes are determined by the peculiarities of the plant. Why malformations occur so abundantly in the flower whilst they are comparatively rare, for example, in roots, may find its explanation in the following[2]:—

1. The primordia of organs arise at the vegetative point of the flower rapidly after one another and commonly in great numbers closely over and beside one another.

2. Organs of different construction, sepals, petals, and others, are thus laid down at short intervals.

3. The more the organs of a plant are aggregated at their points of origin the easier it is for malformations to occur, as very small disturbances suffice to cause changes in the passage of the organ-forming material into the primordia. A normal construction of so complex an aggregation of organs as the flower can only take place when all movements of material and all cell-divisions follow with an almost mathematical accuracy. When, for example, some molecules of such substances as are required for the formation of anthers deviate only the 1/1000 mm. to the right or to the left from their normal path, or in their passage into the vegetative point of the flower are delayed or hastened, they may enter into, and induce a partial anther-character in, a carpellary leaf or a petal.

During my investigations into the development of double flowers[3] I came to the conclusion that Sachs' conception made possible the harmonizing of the facts in the simplest way. In every case we have

[1] Sachs, Gesammelte Abhandlungen über Pflanzenphysiologie, ii. p. 1159.

[2] See also Sachs, Über Wachstumsperioden und Bildungsreize, in Flora, 1893, p. 217.

[3] Goebel, Beiträge zur Kenntnis gefüllter Blüten, in Pringsh. Jahrb. xvii. p. 207.

to deal with an increase in the quantity of the material for forming flower-leaves. This expresses itself sometimes in a splitting of the normal primordia of the flower-leaves, sometimes in the appearance of new primordia of flower-leaves, sometimes in the transformation of the primordia of other leaves of the flower to petals with which are associated frequently profound disturbances in the construction of the primordium of the whole flower.

In 1887 Sachs explained[1] that he did not include in his conception of the 'flower-forming material' the whole mass of material out of which a perfect flower or flower-bud arises. 'What I understand is that extremely small quantities of one or of different substances (chemical combinations) arise in the leaves, and these then so influence the plastic materials which as we know flow into the vegetative points that they assume the form of flowers. These flower-forming materials may act like ferments upon a large mass of plastic substance whilst their own amount is extremely small.' This conception conforms entirely with the views upon transformation to which we have been led above. It rests further upon the ground of 'epigenesis'; just as the configuration of a starch-grain is conditioned by the material nature of the starch-producing plant, so also is the form of organs affected by the plastic material for their construction.

Beyerinck[2] also, as a result of his studies of the formation of galls, was led to the same conclusion as Sachs. He assumed that the gall-forming material excreted by insects has the character of an enzyme, '*growth-enzyme*' he called it, which so influences the protoplasm of the host-plant that the formation of a gall ensues. Following the lead of Sachs he also assumed that such 'growth-enzymes' are present and active in the normal formation of organs, only in this case they are formed by the protoplasm of the plant itself. As these enzymes must obviously be different for different organs, Beyerinck's view conforms with that of Sachs.

This short reference to these general questions must suffice here. In this difficult field we can only as yet deal with similitudes; we are unable to treat in detail complete theories. Every general interpretation however will be the more fruitful the more it makes possible a clear issue for further experimental investigation.

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[1] Sachs, Gesammelte Abhandlungen über Pflanzenphysiologie, i. p. 307.

[2] Beyerinck, in Botan. Zeitung, 1888.

FIFTH SECTION

THE INFLUENCE OF CORRELATION AND EXTERNAL FORMATIVE STIMULI UPON THE CONFIGURATION OF PLANTS

BRANCH OF THE ROYAL ASIATIC SOCIETY

THE INFLUENCE OF CORRELATION AND EXTERNAL FORMATIVE STIMULI UPON THE CONFIGURATION OF PLANTS

INTRODUCTION.

I HAVE shown in the preceding Section that external circumstances often exercise a profound influence upon the formation of organs; thus the formation of a shoot may be induced upon the leaves of Pteris quadriaurita in a position where no such shoot normally appears through the attack of a parasitic fungus, and where this occurs the structure and configuration of the leaf of the fern become changed[1]. In this case, a definite external factor, the parasite, acting upon the definite peculiarities of the protoplasm of the host-plant has influenced the formation of organs and their further development; in like manner the normal formation of organs is also determined and influenced by external factors, assuming of course that, as is necessary for all life-processes, the general conditions for life are present. The investigation of these factors however falls within the province of experimental physiology, as does also the study of those special cases in which the *unfolding* of organs from their primordial condition, or their development generally, takes place only under definite conditions acting as stimuli; the consideration of these is not a part of our task here. It is, for example, of no moment to organography that the germination of the seeds of Orobanche takes place only when they are brought into contact with the roots of a host-plant, or that the spores of the liverworts will, according to Leitgeb, only germinate in the light. If, on the other hand, it were shown that the configuration of the seedling is different according to the greater or less intensity of the light, this would be a fact of the highest importance for organography because it would show a direct dependence of configuration upon external conditions. There are of course no absolute limits to be

[1] See p. 193.

drawn between our subject and physiology, but we shall always endeavour to consider our facts from the organographical point of view, as is done by Hofmeister in his classical 'Allgemeine Morphologie,' a work which expressly adopts an experimental treatment of morphological questions, and thereby stands out in striking contrast with the idealistic morphology of its day.

There are two branches of experimental organography which we have to consider:—

I. The reciprocal influence of organs upon one another; this is termed *correlation*;

II. The influence of external factors which, with Herbst[1], we may call *formative stimuli*. In the Fourth Section dealing with malformations examples of such formative stimuli have been cited.

I. CORRELATION[2].

The facts mentioned in the chapter upon regeneration[3] have shown that the organs of many plant-bodies can under favourable conditions continue their life after being separated from the parent plant. Thus in the operation of budding we remove buds, in the case of grafting we take off whole shoots from the tissues with which they were previously connected, and unite them with others; leaves also and roots may be removed from a plant and placed upon another, either of the same or of a different species, and they grow on and continue their life-phenomena.

We might be led to conclude from these facts that the organs possess a far-reaching independence one of the other. Careful research however shows that this is not the case and demonstrates the existence of a reciprocity between parts of the plant-body; the size and construction of one organ is frequently determined by those of another[4]. These reciprocal

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[1] Herbst, Bedeutung der Reizphysiologie für die Ontogenese, in Biol. Centralbl., 1895, p. 721. I specially direct attention to this excellent treatise.

[2] See Goebel, Beiträge zur Morphol. und Physiol. des Blattes, in Botan. Zeitung, 1880, p. 753; Id. Über die gegenseitigen Beziehungen der Pflanzenorgane. Berlin, 1884—this paper has been much used in preparing the account given here; Id. Zur Geschichte unserer Kenntnis der Korrelationserscheinungen I, in Flora, 1893, p. 38, and II in Flora, Ergänzungsband, 1895, p. 195, where the older literature is cited.

[3] See p. 43.

[4] One might also say, through its relations to the system of organs to which it belongs, a system which forms to a certain extent an interdependent whole and endeavours if it be injured to reconstruct itself again as far as possible. Of the existence of a 'system' we are assured from the facts of correlation, and it appears to me to be of subordinate importance whether, with Herbst, we see in injuries such as the severance of the top of a conifer the 'alteration of the system' or a direct influencing of the organ. The influence of the separation of the top is that the position of the uppermost lateral shoots in the 'system' becomes different and in conformity therewith their growth and relationships of configuration are changed.

influences we term *correlations*. We can only speak with certainty of such a condition when it can be proved experimentally, for in many cases the construction of an organ stands in evident relation to that of another, but we are unable to say whether this is direct or indirect. In the species of Phyllanthus which bear leaf-like lateral branches the leaves on the chief shoot are usually reduced to scales, but this result may be reached in different ways :—

(*a*) The lateral shoot, which resembles a pinnate leaf, may directly affect the primordium of the leaf arresting its growth, or—

(*b*) The foliage-leaves of the chief axis may become more or less functionless because of the leaf-like construction of the lateral shoot and therefore take on an arrested form.

In the first case only is there a direct correlation. As it is of the utmost importance for organography that such correlations should be established, I shall in what follows cite some of the best-known examples.

The influence which is exerted in correlation is either *quantitative* or *qualitative*, but there is no sharp line between these. The quantitative is the simplest and will be first illustrated.

1. Quantitative Influence of Correlation.

Where quantitative correlation occurs either the development of the primordium of an organ is entirely suppressed by another organ, or the size to which it can attain is limited by the correlation. This quantitative correlation has been also termed *compensation of growth*.

Every plant-body forms more primordia of organs than it is able to bring to maturity. Just as by far the greater number of seeds which are annually formed are destroyed, sometimes because they do not find favourable environment for their development, sometimes because they are overcome by other organisms in the 'struggle for existence,' so also some of the primordia of organs remain undeveloped because the plastic material which they require for their unfolding is taken by others which exercise a stronger attraction upon it. This rivalry appears as a 'struggle,' particularly in the formation of the propagative organs. The fruit in the case of the oak, the beech, the lime, encloses a relatively very large seed ; in the ovary a much larger number of ovules is found, as many as six in the oak, and ten in the lime. The act of fertilization may be effected within each of these ovules and they are all capable of developing into seeds, and occasionally more than one seed is formed ; but commonly at a very early period one single ovule takes the lead and absorbs all the plastic material streaming into the young fruit and the others are arrested in their development by it and finally are suppressed. What causes determine which shall be the favoured ovule are at present unknown, nor are we able to say whether that

ovule which is first fertilized is the one, or whether other factors come into operation.

Even more striking are the incidents in the development of the seeds of many conifers. In the pine we find three to five eggs in the ovule, each of them capable of fertilization. Let us suppose that three of them are fertilized: three embryos are produced in the first instance, and each of them then splits into four partial embryos each of which might develop to a complete embryo and there would then be twelve embryos in a seed; but subsequently only a single one is found; it has gained the upper hand and brought about abortion of the others to the extent that in the ripe seed we can scarcely find even their compressed remains. This splitting of the primary embryo is evidently useless; yet further more accurate research may perhaps prove that the arrested partial embryos play to a certain extent the part of haustoria, that the nutriment in the endosperm may be passed on by them in a form which can then be quickly used by the privileged embryo.

The several fruits produced by the flowers in a many-flowered inflorescence engage in a struggle of the same kind as that witnessed between the several seeds (or the primordia of embryos) included within the fruit. It is quite common to find that the plastic material is not sufficient to bring about the unfolding of the youngest last-formed flowers at the end of the inflorescence; whilst usually all the organs are laid down in them, they are arrested because the older flowers have already begun the formation of their fruit and therefore demand all the available plastic material which would otherwise have flowed on to younger flowers. If one removes at an early period the fruits as they are forming in such an inflorescence, the younger flowers which in normal circumstances would have been arrested will be developed; this may be readily observed in Borragineae, Oenothera biennis, and other plants. This correlation is the less evident the more favourable are the conditions of nutrition of the plant. In the examples we have just mentioned the flowers which usually become arrested may be regarded from the utilitarian standpoint as reserves which may come into action in the case of the failure of the act of fertilization in the older flowers; but one must carefully distinguish such cases from those where the last flowers are arrested from the outset in the bud, as happens in many grasses. Such arrested flowers, which are found in many different stages of development, are, so far as we as yet see, quite useless structures.

We find also in the vegetative region examples of the temporary or permanent arrest of development through correlation. In trees and shrubs with a periodic growth the axillary buds on the twigs of any one year only shoot out in the succeeding year. By a timely removal of the leaves the development of these buds into shoots may be brought about in the year of their formation, and this happens in nature in plants whose leaves

exhibit transformation or reduction, for example, in Berberis in which the leaf-thorns have short leafy twigs in their axils, and also in Pinus where the leaves on the long shoots are reduced to scale-leaves.

Long ago, de Candolle [1] referred these phenomena to the withdrawal by the leaves of the 'sap' from their axillary buds. Wiesner [2] advanced the analogous explanation that the older and more strongly transpiring parts, here the axillant leaf of the bud, withdraw the water from the younger parts and therefore hinder the sprouting of the shoot. A similar explanation has been given of the abortion of the apex of the annual shoots of Ulmus, Fagus, Carpinus, Tilia, and other trees; in these plants the leaves gradually diminish in size towards the point of the shoot the end of which finally withers and falls off, and this non-persistence of the terminal bud has been ascribed to the abstraction of water by the older parts. In my view other factors are also concerned in these phenomena.

Correlation with other buds is also a point that must specially be considered in connexion with the development of a bud. Without defoliating an annual shoot which is still growing, we can cause its buds to shoot out by removing its apex: the buds which are nearest the cut surface then shoot out, as has already been explained, those which lie towards the base of the shoot become arrested in their development, they remain undeveloped or grow out into short twigs. To this point I shall refer later. That the buds which remain undeveloped may be of subsequent use in the event of injury to a tree has already been stated. The provision of many plants in this respect is well shown in seedlings of Juglans regia. Here a large series of buds placed one above the other up to as many as eight is found above the axil of the cotyledon although there is usually only *one* bud in the axil of each of the other leaves. No one of these numerous buds develops into a twig in the normal and undisturbed development of the seedling, and after some years they are no longer visible. This arrest is not brought about by an 'abstraction' of the sap by their subtending leaf, because here the cotyledons remain hypogeal; it is due to all the available food-material being devoted to the development of one terminal bud by which the stem increases in length. If this bud be destroyed whilst the lateral buds are still capable of development, that is in the first or second year of the plant, then one or more of the lateral buds will shoot out and the further development of the seedling is secured. Many cases of developmental arrest on vegetative shoots and on flowering shoots can be traced to correlation of growth.

This holds good also for leaves and parts of leaves. The size which the leaves attain is much greater when each single leaf has a plentiful supply

[1] De Candolle, Physiologie végétale, p. 767.

[2] Wiesner, Der absteigende Saftstrom und dessen physiologische Bedeutung, in Botan. Zeitung, 1889, p. 1. The literature is not given in this paper.

of food-material than when a fixed quantity of food-material is distributed over a number of leaves. It is in consequence of this that leaves upon stool-shoots are much larger than normal, and that organs which are abortive on the ordinary leaves often appear upon them. Thus on stool-shoots of Robinia Pseudacacia the stipelles develop into leaflets[1], and in Sambucus nigra the stipules which are commonly much reduced may become leaf-like.

The behaviour of the stipules of many plants is most instructive. Their size depends upon the influence of the leaf to which they belong. If the leaf-primordia are removed above the stipules at the earliest possible moment a remarkable increase in size of the stipules takes place as the following figures will show.—Of two plants grown together in a pot from equally heavy seeds, one had the leaves left untouched, in the other they were removed at the earliest possible moment; the surface measurements of the stipules were as follows:—

	Plant with leaves.	*Plant without leaves.*
1. stipule	141 □mm,	239 □mm,
2. „	172 „	561 „
3. „	165 „	920 „

Occasionally we find in nature misformed plants in which the leaves are completely aborted whilst the stipules are greatly enlarged, and the latter condition is a consequence of the former. We are able readily to recognize this in Lathyrus Aphaca whose leaves are transformed into tendrils, whilst their usual function is performed by the uncommonly enlarged stipules (see Fig. 110). It is not however possible to prove such a correlation in all plants provided with stipules, and we may perhaps account for this by the fact that the stipules lose their capacity for growth at an earlier period than can be reached by experimental interference. We cannot, for example, promote an enlargement of the stipules in Phaseolus multiflorus and other plants by the experimental method just referred to.

I have already said that relationships of correlation have probably to do with the unequal formation of the leaflets of compound leaves[2]. This dependence certainly exists in the case of the cotyledons of Streptocarpus. In this plant the two cotyledons attain very unequal dimensions, the one remains small, the other becomes a large foliage-leaf lying upon the ground; if the large cotyledon be removed at an early period, or if its growth be restricted by enclosing it in plaster of Paris, the other cotyledon develops to take its place[3].

[1] See Part II of this book.

[2] See p. 127.

[3] F. Hering, Über Wachstumskorrelationen infolge mechanischer Hemmung des Wachsens, in Pringsh. Jahrb. xxix. p. 142.

I have elsewhere[1] pointed out that the size attained by a leaf may be dependent upon correlation with its shoot-axis. In illustration of this we have the behaviour of many climbing plants in which the rapid and strong elongation of the internodes causes a transient or permanent arrest of the development of the leaves. The smallness of the leaves of etiolated shoots is, at least in many cases, no direct result of the influence of light, because if the upper part of a shoot of Phaseolus multiflorus is confined in a dark chamber, and only one leaf is left upon it, and at the same time all the vegetative points of shoots are removed from it at an early period, the leaf in the dark attains the same size as the leaves on the part of the shoot in the light[2].

It is probable that similar correlations also exist between the leaf-structures in the flower. In the flag-apparatus formed by the peripheral flowers of the inflorescence of many Compositae, in Viburnum Opulus, and species of Hydrangea, the corolla, or in the case of Hydrangea the calyx, becomes greatly enlarged whilst the stamens and carpels are either functionless or entirely wanting, and the conjecture is fully justified that a direct compensation occurs here, in other words, that the growth of the corolla or calyx causes the arrest or abortion of the sporophylls. It is true this compensation has not been experimentally proved, but other similar cases make its existence likely. Such similar cases are found, for example, in the abortion of the whole flower as we see it in Muscari comosum, the fasciated garden-form of Celosia cristata, the cauliflower and other cases. In Muscari comosum the higher flowers of the inflorescence form the flag-apparatus, their stalks are much longer than those in the lower inconspicuous flowers and are coloured blue, and the sporophylls are arrested in

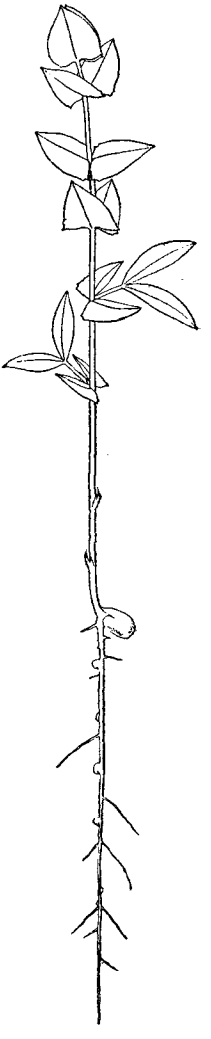

FIG. 110. Lathyrus Aphaca. Seedling plant. The lamina is developed on the two lower foliage-leaves only, and the stipules are much smaller in these leaves than in the succeeding ones in which the lamina is suppressed; higher upon the stem tendrils replace the leaves.

[1] Goebel, Pflanzenbiologische Schilderungen, i. p. 236.

[2] Jost, Über die Abhängigkeit des Laubblattes von seiner Assimilationsthätigkeit, in Pringsh. Jahrb. xxvii. See also with reference to phenomena of etiolation—Godlewski, Zur Kenntnis der Ursachen der Formänderung etiolierter Pflanzen, in Botan. Zeitung, 1879, p. 81. In the cultivation of the tobacco-plant the size of the leaves is greatly increased by topping of the chief shoot and removal of the lateral branches; see Wollny, Untersuchungen über künstliche Beeinflussung der inneren Wachstumsursachen, in Forschungen auf dem Gebiete der Agrikulturphysik, viii.

various stages of development in consequence of the conversion of the stalk into a flag-apparatus. In the inflorescence of the cauliflower the flower-stalks are abnormally thickened and fleshy; and in Celosia the axes of inflorescence are expanded into a broad band upon which many abortive flowers are formed beside normal ones. The list might be extended; Rhus Cotinus, for example, will suggest itself. There are however no experimental proofs of any of these cases and in the absence of them our conclusions are merely conjectures, although no doubt very probably correct; and the same must be said regarding the conclusion that in seedless fruits of pine-apple and cultivated banana the abortion of the seeds is caused by the increased development of the flesh of the fruit.

The cases last mentioned lead us to a consideration of the relationships which obtain between the flowers or the organs of reproduction in general and the vegetative parts. On the one hand there are many cases which show us that a restriction of vegetative development may be bound up with the formation of the reproductive organs or their products; as examples of this we have the dying of the prothallus of a fern after the embryo is formed, and the death of annual plants following upon the formation of their flowers and seeds. On the other hand the formation of the reproductive organs may be suppressed in circumstances which provoke a luxuriant development of the vegetative organs, whilst a restriction in the growth of these may bring about the formation of the reproductive organs. In this part of the subject a considerable amount of knowledge has been accumulated [1] which it is not my intention to bring together here, as it more properly belongs to the physiology of reproduction. Some few examples will serve my purpose.

The Coniferae in particular furnish us with examples illustrating the favourable influence of restricted growth upon flower-formation, as I have already pointed out. Transplanted spruces, for example, flower much earlier than is normally the case, although the flowers do not usually produce fruit, and I have seen similar phenomena in Thuja occidentalis; on poor soils transplanted plants are profusely covered with flowers. Similar instances are familiar to every gardener. Annual plants will reach the stage of flowering much later, other conditions being equal, if they are growing in rich soil where a luxuriant vegetative growth is possible, than will be the case if they have but little nutriment available; nutrition acts as a stimulus, to use a modern expression, which compensates for a longer vegetative development and which naturally also makes possible a richer formation of seeds [2].

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[1] With regard to the lower plants see Klebs, Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen. Jena, 1896.

[2] See also p. 142.

If a plant should form no reproductive organs but exhibit a luxuriant vegetative growth, the latter may be either the cause or the consequence of the suppression of the reproductive organs. Both cases occur.

In illustration of the former I may quote the behaviour of many water-plants which, like species of Marsilia, Riccia fluitans, and others, do not form their reproductive organs so long as the external conditions are favourable for growth, but should they grow as land-plants the luxuriance of the vegetative development is restricted and the reproductive organs arise normally. H. Müller [1] has also conjectured that the explanation of the fact that plants which shoot in a higher temperature than normal often produce 'blind' flowers may be found in the leafy shoots depriving the flower-buds of nourishment. A similar explanation may be given of the frequent cases in which the formation of seed is arrested; in Lilium candidum, for example, seeds are never formed; in plants like Ranunculus Ficaria provided with means of vegetative propagation seeds are seldom produced. More than two hundred years ago K. Gesner showed that flower-stems cut off from Lilium produced seeds [2]; in the normal condition the seed-formation is hindered because the plastic material which might be used for the seeds streams into the bulb where it is turned to account in the formation of bulbils for asexual reproduction. In Lachenalia luteola also Lindemuth [3] found that notwithstanding artificial pollination no seeds were formed, but that their production could be brought about by cutting off the flower-stalks; and Van den Born [4] has proved the same in Ranunculus Ficaria.

The opposite case—that an increase of vegetative development is a consequence of the suppression of the reproductive organs or of their incomplete development—is illustrated in many double-flowered plants. In the vicinity of Munich, Cardamine pratensis occurs abundantly with double flowers. The plant multiplies copiously by buds which are developed upon the basal leaves and out of the apex of the double flowers, and thereby this bud-bearing form which has entirely lost seed-formation [5] has partly replaced the normal seed-forming plant—a condition of things which could only be possible in a climate with so great a rainfall as that of the high plain of Upper Bavaria. The example of Isoetes

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[1] H. Müller, Beitrag zur Erklärung der Ruheperiode der Pflanzen, in Landwirtsch. Jahrb., 1886.

[2] See Jost, in Botan. Zeitung, 1897, p. 17.

[3] Lindemuth, Über Samenbildung an abgeschnittenen Blütenständen einiger sonst sterilen Pflanzenarten, in Ber. der deutsch. Botan. Gesellsch. xiv (1896), p. 244.

[4] Van den Born has induced the development of fruit in Lilium candidum and in Ranunculus Ficaria by removing from the former the bulb-scales and from the latter the small basilar tubercles. See La Belgique Horticole, 1863, p. 226.

[5] Adventitious shoots may be formed also on the normal form, but the absence of seed-formation sets free a larger amount of plastic material.

lacustris I have described [1], in which in definite circumstances the formation of sporangia is suppressed, may be cited here, likewise the case of the old prothalli of Doodia caudata upon which the sexual organs are abnormal and apogamous shoots are developed; probably in other cases in which these appearances are seen the process is the same.

2. Qualitative Influence of Correlation.

The relationships of direction due to the qualitative influence of correlation must next be referred to. Such relationships are conditioned primarily by reaction to outer stimuli, such as geotropism and others, but correlation also is an important factor. This is specially the case where a plagiotropous lateral shoot springs out of an orthotropous chief axis.

The relationships are seen most simply in the roots. When speaking of regeneration I stated that the severance of the tip of the chief root influenced in many cases the growth of the lateral roots; that lateral root which stands next the cut surface is devoted to the elongation of the primary root and takes on therewith its peculiarities, that is to say, capacity for growth and branching becomes increased and the former lateral root becomes the foundation for the further differentiation of the root-system.

The conifers supply the most instructive examples for the *shoot-system.* The dorsiventral construction of the lateral branch in the spruce has been depicted above, but this is only brought about by its plagiotropic growth which is a consequence of correlation. If one cuts off the top of the main shoot, the nearest lateral shoot [2], always supposing that it is not too old, grows erect and takes on a radial construction quite like that which is characteristic of the chief shoot. We must recollect however that the dorsiventrality induced in the side-shoots through their plagiotropous growth is to a certain extent differently fixed in the several forms. In the firs this substitution of a lateral shoot for the terminal one is less easy than in the spruce; it would appear that it takes place better the stronger the plant and the younger the shoots. Should a side-shoot not become erect, one or more radial shoots issue from its base and one of them takes the place of the terminal twig. Araucaria does not possess this capacity of transforming a dorsiventral lateral shoot into a main terminal one; in this genus the lateral shoots are branched only in one plane in by far the greater number of cases, and so far as we at present know this peculiarity appears to be fixed in them from the beginning. It is of course possible that in Araucaria, in accordance with what has been already said about Phyllanthus [3], the lateral

[1] Goebel, Über Sprossbildung auf Isoëtesblättern, in Botan. Zeitung, 1879, p. 1.

[2] Or it may be many lateral shoots.

[3] See p. 97.

shoots in the vegetative points have their dorsiventrality merely *earlier* and more firmly induced than usual, and that very young lateral shoots are capable of replacing a terminal one. It may be mentioned here that the spur-shoots of species of pine may in like manner be caused to develop into long shoots, and the same holds for other cases.

The potato furnishes an example of a specially plastic subject, and Knight carried out a number of very interesting experiments upon the plant. The tubers of the potato are underground lateral shoots which have been transformed into reservoirs of food. Their transformation is brought about under the influence of the material which flows downwards from the leaves in which it is formed. If the aerial shoots are cut off from a potato-plant before the formation of tubers is begun the subterranean shoots grow into the air and become leafy shoots. They are nothing else then than leaf-shoots which on account of their position in the whole shoot-system of the plant have become accustomed to an underground life, and subsequently under the influence of the material supplied from the aerial leafy shoots have become transformed into tubers. If this double influence be removed they take on at once their original character and replace the aerial organs which have been removed. It is possible also, as Knight has shown, to cause aerial shoots to form tubers. This takes place if at an early period the subterranean stolons are removed, or their connexion with the aerial parts be interfered with. Knight carried his experiments so far that he was able to cause the formation of tubers on the top of the aerial shoots—the points which are furthest separate from the normal position of formation of tubers[1]. It is also to be noted that want of light is favourable to the formation of tubers.

The formation of branch-thorns, in which a shoot-axis by abortion of the leaves and cessation of growth in length becomes a thorn, is quite comparable with the formation of tubers. If one cuts off the end of a branch the side-shoot of which would have developed in normal vegetation into a thorn, this side-shoot will become an ordinary leafy shoot, not a thorn.

The influence of correlation in the configuration of the *leaves* is known in a number of cases. The sporophylls of Pteridophyta will be discussed in this connexion in the special part of this book; but I may here mention that they frequently deviate in form, size, and direction, from the foliage-leaves. These deviations are chiefly occasioned directly by the appearance of the sporangia on the sporophylls[2]. The primordia of the sporophylls

[1] See also De Candolle, Pflanzenphysiologie, i. p. 130; Vöchting, Über die Bildung der Knollen, in Bibliotheca botanica, Heft 4. Cassel, 1887.

[2] This influence naturally takes effect often very early; before the sporangia are visible as such the material changes have occurred which lead to their construction and these changes may affect the configuration of the primordium of the leaf.

conform in the first instance entirely with those of the foliage-leaves, and it is the appearance of the sporangia which induces their different development from that of the primordia of the foliage-leaves. Comparative observations have made it certain that such a correlation exists [1]. The experimental proof which has been furnished in the case of Onoclea Struthiopteris bears upon this point [2]. By the removal of the foliage-leaves the formation of sporangia can be entirely or partially hindered, and the primordia of the sporophylls can be forced into development as foliage-leaves [3].

The same is the case in bud-scales. Those which serve as protective organs to the bud during its resting period differ from the foliage-leaves of the plant to which they belong only to an insignificant extent in size and form; they have, even where the foliage-leaves are much segmented, only the form of simple scales, a form which for their work as 'covers' to the bud is the most favourable. There are three methods of transformation of the primordia of the foliage-leaves to bud-scales: usually the bud-scale is formed out of the basal part of the leaf-primordium, the leaf-base, whilst the primordium of the blade is arrested and the petiole is not developed; or the primordium of the blade is arrested and the stipules develop to bud-scales; or finally the whole leaf is transformed into a bud-scale. In all three forms it is possible to show that the transformation can be hindered. This happens where buds which are destined for a succeeding year develop into shoots in the year of their formation, and according to the moment at which this takes place will the bud-covers become foliage-leaves, or, if the transformation had already begun, intermediate forms between bud-scales and foliage-leaves will be found.

As a last illustration I may mention that one can often hinder the transformation of the leaflets of the pea into tendrils if one removes the other leaves.

All these examples, to which many others might be added, show that correlation plays an important part in the formation of organs, and this

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[1] See what I say on this subject in my 'Vergleichende Entwicklungsgeschichte der Pflanzenorgane.'

[2] Goebel, Über künstliche Vergrünung von Farnsporophyllen, in Ber. der deutsch. botan. Gesellsch. v (1887). Figures will be found in Annals of Botany vi, plate xxii.

[3] In Selaginella also a correlation is observable between the formation of sporangia and the formation of the leaves (and the whole shoot clad with sporophylls). I have already proved that in Selaginella Lyalli the sporangiferous spikes, which differ from the vegetative shoots in the form of the leaves, may develop into vegetative shoots if the formation of sporangia be arrested. Behrens has recently shown that this regularly happens if sporangiferous spikes are used as cuttings, and he concludes that the growing out of the apex of the spike causes the suppression of the sporangia. (See Behrens, Über Regeneration bei Selaginella, in Flora, Erg.-Bd. 1897, p. 159.) To my mind a better explanation is that the severance of the spike causes a disturbance in the formation of the sporangia which permits of the further vegetative development.

becomes the more significant when we remember our present limited experimental experience. The facts that have been here shortly brought together also furnish proofs in support of the view of the process of transformation enunciated in the earlier pages of this book.

II. INFLUENCE OF EXTERNAL STIMULI.

The special character of the living substance of the egg determines the kind and manner of formation of organs of the plant which springs from it. I have however already pointed out when speaking of juvenile states, of relations of symmetry, and of malformations, that external agencies may influence the configuration; they act as stimuli whose influence depends upon the capacity of reaction of the individual plant. This capacity of reaction may change in the course of the development of the individual [1]. A strong growing shoot of Bryopsis behaves quite differently from a less strong one when the whole plant is inverted; the latter suffers a transformation, the former does not. Further, the phylogenetic development of the plant kingdom is, although we cannot here enter into detail on this matter, evidently to be traced to intrinsic causes in the nature of the living substance and to the influence of external factors upon these. This external influence is in many cases direct and is still observable, but in others we must assume that it has been inherited and is then only to be recognized by the clue of analogy. When we see, for example, that the aerial roots which contain chlorophyll of many orchids become flattened upon the side directed to the light only under the influence of light, whilst in other roots this may be observed although they are in darkness, and again, that the dorsiventrality of many organs is directly influenced by external factors, whilst in others it is inherited, it is permissible to conjecture that in the latter of each series of cases the formation of organs was originally influenced by external stimuli and that the effect was then transmitted. The wonderful conformity which the configuration of plants exhibits even in the most different systematic groups confirms this assumption.

The dependence of the formation of organs upon external factors has often a utilitarian character. The seedlings of many liverworts and ferns, for example, are threadlike in feeble light but form cell-surfaces in light of greater intensity, and it is quite clear that the first peculiarity enables them to reach more favourable conditions of illumination, whilst the second enables them to maintain a more intense capacity of assimilation.

[1] See what was said at p. 171, upon the reversion to the juvenile form.

It is however possible to assume that the organisms were from the beginning dependent in the formation of their organs upon external conditions, and that only those of the relationships of dependence which were of use have been retained through the survival of the fittest. This appears to me specially to be supported by the circumstance that often the factor which causes a definite relationship in the formation of organs is not by any means that to which the organ itself is 'adapted.' I have already referred to such examples. The archegonia of the prothalli of ferns arise upon the shaded side. This is of itself a fact of indifference for the function of the archegonia, because in many other cases they arise on the illuminated side of a dorsiventral thallus, as in Pellia and others, or they are distributed equally all round, as in prothalli of Lycopodium, the archegoniophore of the prothalli of Trichomanes, and elsewhere. In the prothalli of ferns however the position upon the shaded side is of advantage because it finds there most easily drops of water which are necessary for the opening and for the fertilization of the archegonia.

A further peculiarity which must be noted here is that one and the same relationship of configuration may be brought about by different external influences. The motile developmental stages of Myxomycetes —swarm-cells, amoebae, plasmodia—for example, have the power to pass over into the resting condition, a stage in which they are very different in configuration from what they were before. The arrest which this change causes can be brought about also by slow drying as well as by other external influences, such as unfavourable nutrition. In correspondence with this I may also mention the aquatic spermaphyte Myriophyllum[1], whose peculiar resting condition, which usually develops in the form of a winter-bud at the end of the vegetative period, just like the sclerotium of a fungus, may be called forth at any time by starvation. These plants react then evidently to any unfavourable external condition in this way—they pass into resting stages, supposing always that the necessary plastic material is in existence for such formations. Bacteria also behave in the same way in formation of their spores.

The appearance of 'reversion-shoots,' which exhibit the simple relationships of configuration shown first of all in germination, is brought about in many plants by different conditions which exercise an unfavourable influence on vegetation; in this way arise the juvenile forms of leaves in Sagittaria natans, Veronica cupressoides, and others[2].

The manner in which the stimuli influence the formation of organs and the nature of their effect may be very different; in the simplest cases there is a *directive* influence. We see this in the appearance of roots upon the shaded side and in other features which cannot indeed be altogether sharply

[1] Goebel, Pflanzenbiologische Schilderungen, ii. p. 360.

[2] See p. 172.

separated from those in which the nature and manner of the *construction*, and not merely the position of an organ, are conditioned by the external influence. We may here specially mention that those external conditions under which normally the life-capacity of an organ displays itself, by which, in brief, it is 'determined,' may also as stimuli bring about the appearance of the organs. Roots ordinarily live in a moist substratum in absence of light; absence of light and presence of moisture bring about also formation of roots. Analogous cases will be frequently brought forward in what follows.

A. Influence of Gravity.

Hofmeister[1] in particular ascribed great importance to the influence of gravity in determining the relationships of configuration of plants, and he referred in support of his view to the dorsiventral construction of the lateral shoots of many plants[2], the configuration of the leaf of plagiotropous shoots of Begonia, and others. There is now no doubt that the influence of gravity as a 'formative stimulus' has been greatly over-estimated, and I may refer in this connexion to what has been said in the chapter upon relationships of symmetry and also to what I say regarding the influence of light when what is known about the occurrence of anisophylly is told. Gravity is however in a number of cases of importance partly in relation to the disposition, partly in relation to the construction of the organ.

1. Influence of Gravity upon the Disposition of Organs.

That gravity has an influence of the kind we shall refer to here has been concluded from what is known of the formation of organs in the embryo of the Pteridophyta, especially of the Filicineae. In the fertilized egg in this group there arise the following parts—stem-apex upwards, root on the under side, one or two cotyledons, and a haustorium which is commonly called the 'foot.' It has however been shown that the lie of the embryo in the archegonium is a definite one, and that the disposition of these parts is entirely due to internal causes, neither gravity nor light have anything to do with it[3]. If prothalli which float upon the surface of water are illuminated from below, the archegonia which normally appear upon the under side are developed upon the upper side, yet, notwithstanding this inversion of position, the embryos which arise within them have the normal relationships to them. Leitgeb was only able to prove a very limited influence of gravity upon the dis-

[1] Hofmeister, Allgemeine Morphologie.

[2] Sachs (Text-book, Engl. Ed., p. 208) has shown that a direct effect of gravity upon the arrangement of the parts of the bud in the dorsiventral shoots of some trees (Cercis, Corylus) is impossible.

[3] See Heinricher, Beeinflusst das Licht die Organanlage am Farnembryo? in Mitth. a. d. botan. Inst. zu Graz. Jena, 1888.

position of the embryo of Marsilia[1]. 'The position of the first division-wall of the pro-embryo of Marsilia is so far definite and independent of external relationship that it always falls in the plane of the axis of the archegonium. It is however capable of torsion about the latter, and in the event of the axis of the archegonium deviating from the vertical it assumes such a position that the embryo is laid with an upper half directed to the zenith, the epibasal half, forming the stem, and an under half, the hypobasal half, forming foot and root.' The macrospores germinate in a position approaching the horizontal (Fig. 111); the result of the disposition just indicated is that the stem-apex, *s*, is in every case turned upwards, whilst the root is turned downwards, and in this way all curved growth is avoided which must take place were the disposition otherwise. The macrospores are liable to torsion; in the homosporous ferns on the other hand the prothallus is fixed to the ground.

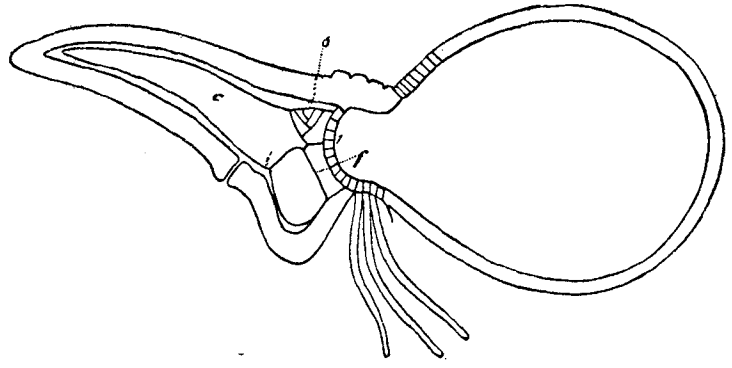

FIG. 111. Marsilia. Half diagrammatic longitudinal section through a macrospore after germination. To the right the macrospore; to the left the prothallus upon which one embryo is developed. The neck of the archegonium is turned obliquely downwards. The pluricellular embryo shows cotyledon *c*, stem-apex *s*, foot *f*, and root. The first division-wall in the fertilized egg is still visible and is indicated by //. The embryo at the stage represented would of course exhibit a construction of many cells, but none of these are shown excepting those of the stem-apex.

The reciprocal position of parts is also in the embryo of Marsilia not displaceable; the foot, *f*, is always as its function requires turned towards the spore in which the reserve-material is stored, the cotyledon and the root are always opposite to it. If the axis of the archegonium be turned so as to be directed vertically upwards or downwards, a condition which really never occurs in nature, gravity cannot of course exercise any

[1] Leitgeb, Zur Embryologie der Farne, in Sitzungsb. d. Wiener Akademie, 1878; Id. Studien über Entwicklung der Farne, ibid. 1879. From what is said in the text it is evident that external stimuli play no part or only a subordinate one in the differentiation of organs in the fertilized egg of the Pteridophyta; the lie of the egg within the female organ is the important matter. The same may be said of the Spermaphyta; the root of the embryo always arises on the attached side of the egg no matter what position this occupies in relation to the horizontal. This is evidently connected with the *enclosed* position occupied by the egg; in the free eggs of Fucaceae external agencies influence the polar differentiation as will be pointed out later.

influence. Leitgeb also states that the influence of gravity is felt in the earliest stages of development in the prothalli of the homosporous ferns. In Ceratopteris, for example, the cell-surface of the young prothallus is vertical and the two-sided apical cell forms segments alternately towards the zenith and towards the apex; dorsiventrality does not yet exist. It appears to me doubtful however whether other factors do not operate here, such, for example, as hydrotropism.

More striking is the influence of gravity on the disposition of the shoots of higher plants [1]. Flat-stemmed species of Opuntia, for example, O. Ficus-indica, produce their later shoots chiefly on the apical parts of the older segments and as a rule out of the edges. That this continuous production of the shoots in the *upper* parts is an effect of the influence of gravity is shown by the fact that if the segments of the stem are inclined obliquely new shoots issue from the *flat* side which is directed upwards. This only takes place however after prolonged influence. I have found also the lateral shoots issuing upon the upper side only of shoots of Echinocereus cinerascens lying on the ground.

The tubers of Thladiantha, one of the Cucurbitaceae, behave in a similar manner. They arise as swellings of the thin root-threads, and in the year after their origin they form adventitious shoots which appear above ground. These shoots arise, as Sachs observed, exclusively upon that side of the tuber which is directed towards the zenith at the time when they are formed; moreover the 'acroscopic' end of the tuber, the one directed to the point of the root, has a preference in respect of these in conformity with its 'inner disposition'—a state of matters opposite to that which commonly holds when formation of shoots takes place on portions of root [2]. Two kinds of causes then are working here together and determine the place of origin of the vegetative points of the adventitious shoot: 'internal causes,' the result of the direction in which the plastic material moves, bring it about that the 'acroscopic' end of the tuber is usually selected for the bud-formation, just in the same way as in the shoot-tubers of the potato the apical end is preferred; and at the same time the influence of gravity causes the shoots to arise upon that side of the tuber which is turned away from the centre of the earth.

The phenomena we have described in Thladiantha lead us naturally to the consideration of the influence of gravity upon the process of regeneration.

The most simple case is that in which regeneration takes place upon a severed portion of a shoot provided neither with primordia of shoots nor with primordia of roots, such, for example, as a long internode

[1] Sachs, Stoff und Form der Pflanzenorgane, Gesammelte Abhandlungen, ii. p. 1159. See also Sachs, Lectures on the Physiology of Plants.

[2] See p. 44.

of a twig of poplar. There is formed here first of all, under favourable external conditions and in consequence of the wound-stimulus, a growth of tissue on both cut surfaces—a callus. What happens subsequently may be shortly told in accordance with the observations of Tittmann[1] upon Populus pyramidalis and P. nigra.—The tendency to formation of roots in the severed portion of shoots of these plants is not great. The formation of callus is quite independent of gravity. Erect cuttings form at the *apical* end a massive callus which bears many adventitious shoots, the *basal* end either remains without any new formations at all or produces roots. This corresponds with what is usual in regeneration, as has been explained above, and is the result of the direction of the current of plastic material in the uninjured plant. Shoots arise at the apical end in conformity with this 'internal disposition.' But external influences are operative, for shoots arise at the *upper* end, roots at the *lower* end. This happens even if the portion of shoot should be inverted, and have its real apical end in the sand and its basal end upwards. In such circumstances the formation of callus was found to be dominant on the basal (free) part, and shoots appeared upon this in about half of the cuttings; the downwardly directed apical part remained without new formations or produced shoots also. Here then in consequence of inverted position shoots appeared upon the basal end of the shoot, but the 'internal disposition' of the apical end to form shoots could not be entirely suppressed. Suppression may however come about through correlation. If, for example, the apical end stands in dry air, whilst the basal end is in water, the latter being under much more favourable external conditions forms the shoots and thereby hinders the formation of shoots at the apical end.

The influence of gravity upon the formation of new shoots is quite evident in the example just mentioned—formation of shoots on the upturned end is favoured. It also becomes noticeable in the formation of organs upon cuttings provided with primordia of shoots, or with primordia of shoots and primordia of roots, although here in less striking degree. Du Hamel long ago observed that on twigs of willow laid upon the ground the roots only appeared upon the under side.

The influence of gravity is felt also in the formation of roots in uninjured herbaceous plants. Suppose we take shoots of Tropaeolum majus and, without severing them from the mother-plant, lay them in vertical and in horizontal positions and cover them with earth so that the long stalked leaves remain in the light, it will be found that the roots sprout out on all sides of the vertical shoots, whilst they appear only on the

[1] Tittmann, Physiologische Untersuchungen über Callusbildungen an Stecklingen, in Pringsh. Jahrb. xxvii. p. 164.

under side of the horizontal ones. Darkness and moisture have here induced the formation of roots; but gravity has determined their disposition on the shoots. Sachs[1] expressly states this when he says that in all living plants, at least in orthotropous shoots, gravity acts, in addition to the earlier arising polarity, in such a way that the roots appear on the end which is directed downwards. As a matter of fact we find that formation of roots takes place in progressive serial succession upon the whole under side in most plagiotropic creeping and clinging shoots; and light also has an effect here in that the roots are arranged upon the under side.

Let us go back to the formation of organs upon cuttings, and particularly those of willow which have been investigated by Vöchting[2]. On cuttings of willow hung up in a vertical position under similar external conditions, buds develop at the apical end, roots round about the basal end. On twigs inclined to the vertical, Vöchting found in general the following behaviour[3]:—If the angle which the twig makes with the vertical be small, the growth of buds is chiefly upon its apical portion and they sprout out from it on every side; with an increase of the angle of inclination the shoots chiefly form upon the apical portion and upon every side of it, *but there is besides an extension of the development along the upper side;* finally, if the twig occupies a horizontal position the shoots on all sides of the apex itself sprout out, but behind this only those upon the upper side develop. The growing out of the buds is here caused on the one hand by polarity, which expresses its influence in the preference given to the apical end; and on the other hand gravity acts, and brings about the formation of the shoots chiefly upon the upper side, whilst the roots appear upon the under. This influence of gravity is well illustrated in Heterocentron diversifolia, a plant whose shoot-axes when used for cuttings possess no primordia of roots but easily form these; if cuttings of it be hung up in the normal position they produce roots only at the basal end, but if the cuttings be inverted the roots arise at a greater or less distance from the base.

Similar phenomena to those observed in severed twigs are seen when shoots sprout upon the mother plant, only of course formation of roots is wanting here[4]. If the weak upper part of a nearly erect one-year-old shoot of a willow be severed before the expansion of the buds has taken place, and then the portion of shoot-axis left behind

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[1] Sachs, Stoff und Form der Pflanzenorgane, Gesammelte Abhandlungen, I, p. 179, and II, p. 1159; Id. Lectures on Physiology of Plants, p. 520.

[2] Vöchting, Über Organbildung im Pflanzenreich, i.

[3] Vöchting, l. c., p. 169. The exceptions and variations are fully dealt with by the author.

[4] Vöchting, l. c., ii. p. 40.

be bent into a different position, the buds upon it to a greater or less distance from the cut surface, now the apex of the shoot, will shoot out. The length and strength of the shoots gradually decrease from the point. If the shoot be bent into a horizontal position then the buds all round the point shoot out, but of the others only those upon the *upper* side of the twig; the buds of the under side remain quiescent or only solitary ones develop. The effect of gravity is quite evident here. In the annual shoots of our trees, as is well known, the buds near the apical end, which in the normal condition is the upper, are furthered beyond those at the base, a point which is material to the formation of the whole skeleton of the tree, and in producing this gravity acts as well as polarity. On the thallus of an alga or a liverwort the lateral shoots nearest the apical region are not furthered beyond the basal ones (see, for example, Fig. 11); the polarity in the regeneration is, as we have seen, conditioned here solely by the direction of the current of plastic material. It is probable that only those plants can develop strong orthotropous shoot-systems in which gravity induces the predominant development of the shoots upwards.

2. QUALITATIVE INFLUENCE OF GRAVITY.

What has just been said leads me to speak of the qualitative influence of the stimulus of gravity in the formation of organs. This often acts in concert with correlation.

The first illustration I shall give is a case investigated by Sachs[1]. Yucca, Cordyline, and allied plants, possess, in addition to their aerial shoots, thick fleshy rhizomes which grow vertically into the earth. In normal circumstances, that is to say, so long as the aerial stem is not injured, these serve as reservoirs of food-material. If however this stem be cut off, leafy shoots are formed at the *upper* (basal) portion of the rhizome, but its terminal bud does not shoot out; but this bud will do so if the rhizome is turned so that the bud is erect. Still, it is not necessary to cut off the aerial parts in order to induce the rhizome to form its shoot. It will develop if the growth of the aerial parts be restricted. This happens usually if the whole plant is placed in an inverted position; but if the chief shoot then instead of becoming restricted in growth erects itself in a negatively geotropic manner, the shooting out of the terminal bud of the rhizome, as well as of the buds at its base, is suppressed[2]. We see then, considering alone the end-bud

[1] Sachs, Stoff und Form der Pflanzenorgane, Gesammelte Abhandlungen, ii. p. 1187.

[2] Vöchting, Über Spitze und Basis an Pflanzenorganen, in Botan. Zeitung, 1880, confirmed Sachs' observation that the rhizome in normal regeneration behaves in respect of polarity like a root; his objections to Sachs' explanation are of no account.

of the rhizome, that it shoots out (1) if the chief shoot be taken away or be restricted in growth, and (2) if this be brought into an inverted position; moreover, we can also cause it to shoot out when it is in its normal position if we remove along with the chief axis all the lateral buds of the rhizome. When we consider the peculiar conditions of life existing here, this example in its fundamentals exhibits the same features as those mentioned in the chapter upon correlation.

The furtherance of the growth of vertical members is specially apparent when we have regard to the difference between chief roots and lateral roots, chief shoots and lateral shoots. That this difference is not exclusively the result of the influence of gravity is quite evident, inasmuch as it is seen in the formation of the chief and lateral axes in Algae, upon whose relationships of configuration gravity has no action[1]. The chief shoot has, when compared with the lateral shoot, the advantage that it is an earlier structure than this is, and therefore its relationships of nutrition and its mechanical claims are points that have to be taken into consideration. On the other hand we cannot deny that axial organs growing in a vertical direction appear to be favoured by this direction; shoots which are inclined at an angle to it develop much more feebly, as has been long known from experiments in fruit-culture, and they have a much greater tendency to produce spur-shoots than those which have a more vertical direction. The facts mentioned on preceding pages lead to the same conclusion, and when we see a lateral root which has come to take the place of the severed chief root[2], or a lateral twig which has become erect, each of them growing now with a much stronger construction and exhibiting other peculiarities, we must admit that besides correlation the stimulus of gravity must also influence them—the 'shoot-forming substances' have evidently the tendency to travel upwards, the root-forming substances to travel downwards. A number of cases that might be mentioned here have already been brought forward when speaking of relationships of symmetry and of correlation, and therefore only a few additional ones need be cited.

Sachs has observed[3]: 'If one allows a five to six-year-old silver fir to grow during a year in an inverted position, that is to say with its apex downwards, there arise upon the dorsal side, the side that was earlier directed downwards but is now the side turned upwards, of the bilateral branches new shoots which are of radial construction and appear like seedling plants.' Evidently there is here a combination of the effect of correlation and gravity. The growth of the chief

[1] See what has been said on p. 36.

[2] See pp. 44, 214.

[3] Sachs, in Flora, 1894, p. 229.

shoot is restricted by the inverted position, the lateral shoots now more removed from its influence develop under the furthering influence of gravity into orthotropous shoots such as we see occasionally upon prostrate individuals and also upon lateral shoots which become erect to replace a severed apical shoot. Just as gravity is a factor which acts along with the early existing polarity in determining the different construction of the buds in the apical and basal regions of the annual shoots, so also does it act in determining differences between orthotropous chief shoots or chief roots and plagiotropous lateral shoots or lateral roots. The behaviour of some succulent plants in which lateral twigs do the work of the arrested leaves, and, in consequence of this, show a different form from the chief shoots, is specially striking and easy to observe. In Opuntia brasiliensis[1] the chief shoot is radial and cylindric; upon it in young plants stand thin flat lateral shoots of about the thickness of a stout pasteboard; on stronger plants the form of the lateral shoot of the first order approaches the cylindric, only shoots of higher order become flat, leaf-like, and of limited duration. It is easy to show experimentally that the difference in the construction of the shoots is connected with their position in relation to gravity[2]. Suppose that the cylindric chief shoot is severed above a strong *flat* lateral shoot, this then becomes erect and grows now as a *cylindric* shoot with the characters of the chief shoot. In like manner *flat* shoots which are placed as cuttings vertically in soil grow usually further as *cylindric* shoots. Euphorbia alcicornis behaves in quite a similar way; it possesses a many-ribbed chief shoot and flat lateral shoots upon which the number of ribs is reduced to two; strong lateral shoots behave here like the chief shoots. If one of the *flat two-ribbed* shoots be taken as a cutting it grows out into an *orthotropous many-ribbed* shoot.

The relationship of the above-mentioned phenomena to anisophylly, so far as our knowledge of the dependence of anisophylly upon outer factors admits, will be discussed below when the influence of light is spoken of. Here I will only say that the earlier view of many authors, like Hofmeister, Frank, Wiesner (the latter has indeed changed his opinion), which made anisophylly a consequence of the influence of gravity, is untenable in its generality, as I have already indicated by the facts brought forward in the chapter upon relationships of symmetry; for it is unquestionably true that, in many cases at least, anisophylly is directly dependent upon the position of the organ where different factors can influence the different sides unequally.

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[1] See Figs. 37 and 38 in my 'Pflanzenbiologische Schilderungen,' i.

[2] See Goebel, in Flora, 1895, p. 113, and 'Pflanzenbiologische Schilderungen,' i. p. 74.

B. Influence of Light.

Light has a much more powerful influence upon the relationships of configuration of plants than has gravity. Here we have not to deal with processes standing in direct connexion with assimilation, but with specific stimulation-effects which at present we cannot satisfactorily explain. In support of this we note that the effects of light are not limited to plants with chlorophyll, that its influence cannot be replaced by the addition of organic food-material, and that it is not the light-rays specially concerned in assimilation which are operative as the stimulus but those of the more refrangible portion of the spectrum.

1. DIRECTIVE INFLUENCE OF LIGHT.

Light determines in a number of cases of dorsiventral organs which side shall be dorsal and which shall be ventral. Different plants react differently in this respect. In some, like the prothalli of Polypodiaceae, the dorsiventrality is reversible at any moment if the side of illumination be changed; in others the dorsiventrality once constituted is permanent and cannot be reversed. I may give some illustrations.

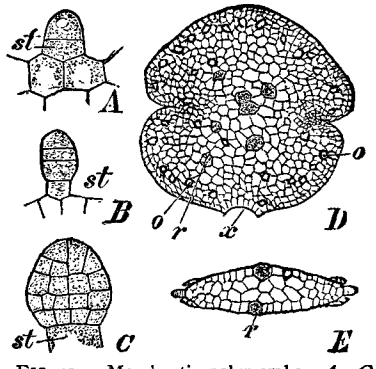

FIG. 112. Marchantia polymorpha. *A*—*C* gemmae in different stages of development; *st* stalk-cell. *D* mature gemma in surface view, on each side is seen a vegetative point which can grow out into a new thallus. *E* transverse section of *D* through the lateral vegetative points; *x* point at which stalk was attached; *o* oil-cells; *r* cells distinguished by their size and contents out of which the hair-roots develop. Lehrb.

The longest known example is that of the plants which are developed from the gemmae of Marchantia and Lunularia. The gemmae which arise in the gemmae-cups, and appear primarily as vertical cell-bodies, are alike in formation on both sides and remain so. They have however at two opposite points on the margin the primordium of a vegetative point, out of which a new dorsiventral thallus may arise if the conditions be favourable (Fig. 112). This thallus has upon its dorsal surface which is normally directed upwards characteristic assimilation-tissue, whilst upon the ventral side hair-roots and scales which serve for the protection of the vegetative point occur. Mirbel[1] long ago recognized that external factors determine the side which is to be dorsal and that which is to be ventral; Pfeffer[2] made

[1] Mirbel, Recherches anatomiques et physiologiques sur le Marchantia polymorpha, in Mém. de l'Acad. des Sciences de l'Inst. de France, 1835.

[2] Pfeffer, Studien über Symmetrie und spezifische Wachstumsursachen, in Arbeiten des botan. Instituts in Würzburg, i. p. 77. See also Zimmermann, Über die Einwirkung des Lichtes auf den Marchantiathallus, ibid. ii. p. 665.

a more accurate research into the matter. We have here to distinguish two things: first of all the appearance of the dorsiventral thallus-structure, and then the outgrowth of the hair-roots for which special cells are laid down on the gemma. The side upon which the light falls is always the dorsal surface, even if the gemma float in water and be illuminated only from below; in such circumstances the surface directed downwards is the dorsal surface. The outgrowth of the primordia of the hair-roots is also influenced, although not so exclusively, by light, if it be sufficiently intense. In darkness the gemmae do not usually develop, and if they do they form no hair-roots, or only a few. Zimmermann found upon twelve gemmae illuminated from below thirty-nine hair-roots on the shaded side and four upon the illuminated side. With reference to the influence of gravity and of contact with solid bodies upon the outgrowth of the hair-roots I must refer to Pfeffer; the gemmae may produce hair-roots on both sides, whilst the thallus which develops out of them is always dorsiventral, and the dorsiventrality is fixed after the influence has lasted three or four days, although by that time the anatomical construction has not yet appeared.

Similar behaviour is exhibited, according to Leitgeb, by the *germ-plants* of different liverworts. The 'germ-disc' of Marchantieae, for example, is not at first dorsiventral; its dorsiventrality depends upon light which determines the side which is to be dorsal, and that which is to be ventral. Once the dorsiventrality is established it is permanent, as in the above-mentioned instance [1].

Dorsiventral prothalli of ferns behave in quite a different manner. In them the dorsiventrality shows itself by the formation on the under side of a cushion of tissue from which the archegonia and hair-roots take origin. The dorsiventrality is here at any time reversible [2]. If a prothallus floating on water be illuminated from below, the new archegonia and hair-roots develop upon the upper side, that which is turned away from the light. If a prothallus be cultivated on a klinostat with the axis of rotation vertical and if the illumination be lateral, it forms archegonia only on *one* side; perhaps this occurs because there is not an equally strong illumination on both sides, or it may be because a bilateral construction is here impossible from 'inner' causes [3]. Upon the advantage to the plant of the archegonia arising

[1] It is clear that as it is a mere accident which side of the gemma is turned upwards, and as there is not always a definite disposition of the germ-disc, it is an advantage that light has a determining influence in the further differentiation.

[2] Leitgeb, Studien über die Entwicklung der Farne, in Sitzungsb. d. Wiener Akad. d. Wissensch. lxxx (1879).

[3] Occasionally prothalli occur bearing archegonia and hair-roots on both surfaces and over a considerable extent of them.

as they do, I have already said something on p. 218. Leitgeb found that relationships similar to those observed in the formation of archegonia occur in the development of shoots on *apogamous* prothalli of ferns; such shoots of course arise asexually and independently of the archegonium[1]. The side to give rise to these shoots is determined entirely by the illumination; and they always arise upon the shaded side like the primordia of archegonia. If the illumination be directed upon the other side after these shoots have once arisen, no further formation of shoots can as a rule be brought about in the side that is now shaded which was formerly the illuminated side, because the existing shoots have claimed all the plastic material of the prothallus; this is different from what happens in the formation of archegonia. A reversal in the position of formation of the shoots by a change in the direction of illumination can only be effected if such change be made when the primordia of the shoots on the first shaded side have not passed beyond the earliest stages. A very peculiar case is that in which the members of *one and the same plant* can be distributed over different sides of a prothallus—on the one side the shoot with first and second leaf, upon the other the first root. This takes place in the prothallus of Pteris cretica if it be illuminated from below at a stage when it has formed young primordia of shoots but no root. Such a case is unquestionably very rare, and Leitgeb's statements do not make quite clear whether the influence is here one affecting merely the *exit* of the root upwards or its origin upon the upper side.

To what has been said above we may add two cases in which the 'polar' differentiation in the germ-plant proceeding from the spore is determined by light. Most spores have polar differentiation; about its cause we know nothing. We see it in the difference between the anterior end and the posterior end in swarm-spores, through which in those Algae which possess a fixed thallus a polar differentiation obtains in the young plantlet, because the swarm-spore fixes itself by the anterior end. The spores of many Bryophyta and Pteridophyta—all those in which they are tetrahedral—indicate plainly the position at which the germ-tube will issue and this is the 'shoot-pole.' The factors which determine the disposition of the poles in germination of radial spores are mostly unknown, it is only in Equisetum and some Fucaceae that we have any information.

The spherical spores, full of chlorophyll, of Equisetum[2] exhibit a similar construction in all their radii. In germination a small biconvex

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[1] Leitgeb, Die Sprossbildung an apogamen Farnprothallien, in Ber. d. deutsch. bot. Gesellsch. iii. (1885), p. 169.

[2] Stahl, Über den Einfluss der Beleuchtungsrichtung auf die Teilung der Equisetum-sporen, in Ber. d. deutsch. bot. Gesellsch. ii. (1885), p. 334; Buchtien, Entwicklungsgeschichte des Prothalliums von Equisetum. Inaug. Diss. Rostock, 1887; Id. in Bibliotheca botanica, viii. Cassel, 1887.

cell is cut off from the spore-cell and this grows into the first hair-root, whilst its larger sister-cell becomes a germ-tube. In the hair-root the chlorophyll gradually disappears and finally only leucoplasts are found. Germination may take place in the dark, but slowly, and then the first division-wall has any position.* If germination takes place in intense light the light affects the disposition of the nuclear division in such a way that the direction of the axis of the nuclear spindle coincides with the path of the light-rays, the two daughter-nuclei therefore lie in this path and the division-wall is at right angles to it. The cell which is turned towards the light is the first cell of the prothallus, the one upon the shaded side, always the smaller, is the primordium of the first hair-root. Diffuse daylight does not exercise a directive influence[1]. Stahl found through a prolonged culture upon the klinostat that a changing direction of the light influenced division in the spores, that most of them were undivided whilst a number of the others were indeed divided but in an abnormal way to form equally large cells. Similar deviations may be reached in other ways. Buchtien found[2] that when the spores were cultivated in concentrated nutrient solution they were divided usually by two walls following one another at right angles, and the formation of a hair-root was often suppressed.

Kolderup-Rosenvinge[3] has observed in the fertilized eggs of some Fucaceae phenomena similar to those noted in the spores of Equisetum. These eggs have no polar differentiation; it is only when germination takes place that the distinction between 'shoot-pole' and 'root-pole' appears, and the filiform anchoring organs develop on the latter. In Pelvetia canaliculata and Ascophyllum nodosum, but not in Fucus serratus, light sometimes, although not always, exercises a directive influence which corresponds with that described in the case of Equisetum. This is most marked in Pelvetia. In these Algae other directive factors, according to Kolderup-Rosenvinge a difference in the amount of oxygen especially, may also influence the polarity.

Amongst higher plants the directive influence of light is specially manifest in dorsiventral shoots.

The branch-system in many Cupressineae[4], for example, Thuya occidentalis, Thuyopsis dolobrata, and others, which possess scale-like leaves

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[1] Buchtien, Entwicklungsgeschichte des Prothalliums von Equisetum. Inaug. Diss. Rostock, 1887. From this it might appear that in nature the influence of light upon the formation of organs in spore-germination is inconsiderable, yet we must consider that within certain limits germination is more rapid the more intense the illumination and therefore the directive influence of light will make itself felt.

[2] Buchtien, l. c., p. 24.

[3] Kolderup-Rosenvinge, Undersøgelser over ydre Faktorers Indflydelse paa Organdannelsen hos Planterne, in Vidensk. Medd. Naturh. Foren. i Kjøbenhavn, 1888; Id. in Revue générale de Botanique, i. p. 53.

[4] Frank, in Pringsh. Jahrb. ix. p. 147.

mostly concrescent with the shoot-axis, is quite dorsiventral and like a leaf in the character of the difference in colour between the upper and the under side. The illuminated side is the 'upper side.' The dorsiventrality is reversible on the new growing parts. The influence of light is here of more significance anatomically than organographically.

Nuphar luteum however shows that dorsiventrality in an organographic sense can be 'induced' through light. In this plant the elongated rhizome creeps in the mud and is densely clothed with leaf-scars. The leaves arise radially in the apical stem-bud, but the insertions of the leaves diverge much further from one another on the under side than they do upon the upper side, thus giving us an approach to what occurs in many other dorsiventral shoots[1]. The roots spring out of the under side, vegetative lateral twigs shoot out from the flanks. If such a dorsiventral rhizome of Nuphar is covered with earth it grows erect and radial until it again reaches the light. The dorsiventrality is here caused by the light which expresses itself in the displacement of the leaf-scars and in the position of the roots. A similar influence of light is found in other Spermaphyta.

In the plagiotropic climbing shoots of the ivy, for example, the roots arise only on the shaded side, although in old plants one often finds the whole surface of the shoot covered with roots[2]. The dorsiventrality is, as Sachs has shown, reversible. Lepismium radicans and other climbing kinds of Cacteae show the same features. It is evident that the roots may be arranged in these plants all round the shoot, but their formation is *suppressed* on the illuminated side. The researches of Sachs[3] have also determined that the exclusion of light, or indeed a diminution of illumination, favours formation of roots, provided, of course, other conditions are favourable. If plants of Phaseolus or Vicia Faba are cultivated in a moist chamber in darkness, numerous adventitious roots shoot out from the etiolated stems at a considerable distance above the surface of the earth; these do not appear in presence of light.

This influence of light upon the formation of roots in the higher plants finds also a parallel amongst the lower ones. On the nodes of Chara which usually bear no roots ('rhizoids'), these may be caused to develop by keeping the shoots in darkness[4]. Investigations are still wanting regarding the behaviour in this respect of the mosses; we do know that the shoots of many mosses are thickly clad with a felt of 'rhizoids' on those parts which are exposed to the light.

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[1] See p. 90.

[2] Possibly this is connected with the formation of a rind which light cannot or can only with difficulty penetrate.

[3] Sachs, Über den Einfluss des Tageslichtes über Neubildung und Entfaltung. Gesammelte Abhandlungen, i. p. 179; Id., Wirkung des Lichtes auf die Blüthenbildung unter Vermittlung der Laubblätter, ibid., p. 229. See also Vöchting, Über Organbildung im Pflanzenreich, i. p. 146.

[4] Richter, Über Reaktionen der Charen gegen äussere Einflüsse, in Flora, lxxviii (1894), p. 399.

The formation of other subterranean organs besides roots is favoured by the absence of light, and in this way the effect of light in their disposition is observable. Thus light retards the formation of tubers on the potato[1]; darkness favours it. Plants in which the formation of stolons has been hindered and from which the possibility is thus removed of the formation of underground tubers may be caused to produce tubers near the apex of their aerial shoots by excluding light from them. Gravity also seems to exercise an influence upon the formation of tubers in this case inasmuch as the tuberous shoots appear on the parts of the chief axis which are turned to the soil[2]. At any rate under normal conditions, light, by retarding the formation of tubers on the aerial parts, has a directive influence and favours the formation of tubers on the subterranean stolons.

Roots and potato-tubers are organs which are 'attuned' to darkness and whose appearance therefore is retarded by illumination. The converse case, namely, the arrestment through feeble illumination of organs 'attuned' to high light-intensities, frequently occurs. When speaking of relationships of symmetry[3], I showed that in spruce the plagiotropous lateral shoots are originally radially branched, and that on account of the want of light the shoots upon their upper side are suppressed; in other needle-leaved trees the suppression of these on the under side also takes place. A like feature is observable in broad-leaved trees, and has a marked influence upon the habit of the whole plant. In Salix incana[4] the leaf-buds develop only upon the side of the shoot which is well illuminated, in this case the upper side; in Populus pyramidalis it is the buds which stand upon the outer side only of the straight erect shoots that are developed.

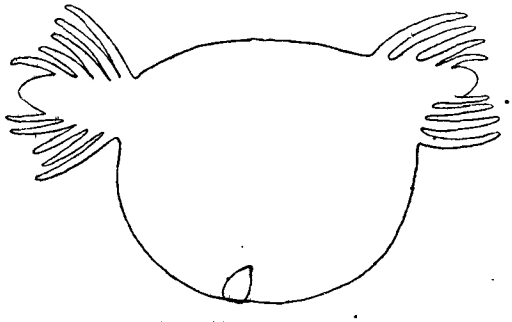

FIG. 113. Thuidium abietinum. Transverse section of a chief shoot. The illuminated side of the axis is flattened, right and left arise two lateral shoots. On the shaded side is the primordium (apical cell) of an undeveloped shoot. Half diagrammatic copy of a drawing by Kienitz-Gerloff.

Light has a share also in the formation of the plagiotropous shoot-system of the mosses, which branches in one plane[5]. There are transitions from the radially branched ordinary shoots to the feathered ones of

[1] Vöchting, Über die Bildung der Knollen, in Bibliotheca botanica, Heft 4 (1887).

[2] For details see Vöchting, l. c., p. 39.

[3] See p. 94.

[4] See Wiesner, Untersuchungen über den Lichtgenuss der Pflanzen mit Rücksicht auf die Vegetation von Wien, Cairo, und Buitenzorg, in Sitzungsber. der Wiener Akad. d. Wissensch., civ (1895), p. 685.

[5] See p. 69, and Figs. 27, 28, 29.

Hypnum splendens, Thuidium, and others. The position of the leaves in these latter forms is still completely radial whilst the branches are arranged in one plane; but there are also on other positions on the shoot-axis primordia of twigs, although, as I think, in less number than the lateral ones. The *primitive constitution* of the branching is then not entirely bilateral, but only the primordia of lateral twigs develop. This arrangement is

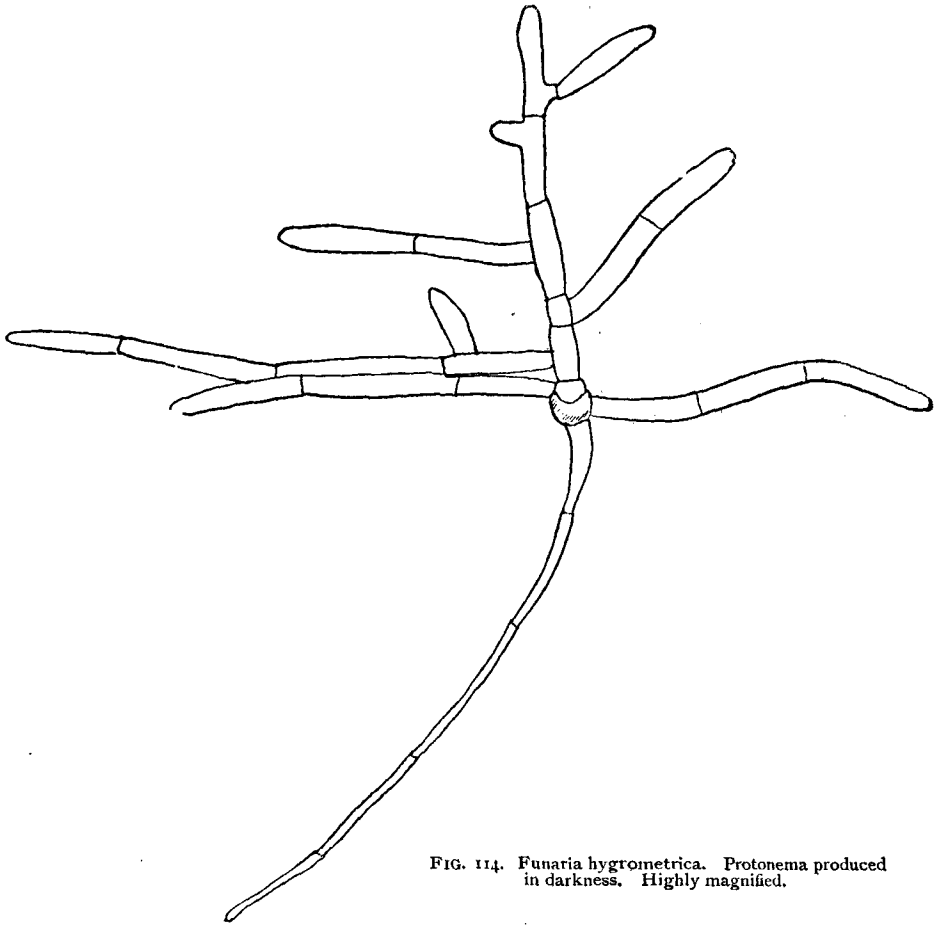

FIG. 114. Funaria hygrometrica. Protonema produced in darkness. Highly magnified.

brought about by light, and the primordia of the twigs of the illuminated side and of the shaded side do not come to development (see Fig. 113). Innovation-shoots of Hypnum splendens developed in cultivation upon the klinostat under a varying illumination produced, according to Coesfeld [1], branches in every direction.

[1] Coesfeld, Beitr. zur Anatomie und Physiologie der Laubmoose, in Botan. Zeitung, 1892, p. 187. The results require confirmation in several directions, especially where the *intensity of light* is concerned.

Sachs[1] has shown that the branching of the protonema of mosses, especially in the case of Funaria hygrometrica, is influenced in a similar manner by light. 'Light acts upon this plant in such a way that the vegetative points of the lateral shoots arise only on the flanks of the mother-shoot when these are illuminated chiefly from one side.' I must however point out that protonemata grown in darkness, and which on account of their nourishment in sugar-solutions had reached a relatively great size, exhibited a two-rowed position of the branches upon the chief axis (Fig. 114), and therefore in this case there exists the tendency to distichous branching, and it is only the plane of this which is determined by the light. That the construction of the protonema is dependent upon outer factors, the case of Ephemeropsis, which I have described, shows[2]. The protonema of this plant is epiphytic on leaves; it bears twigs upon its back and upon its flanks, and from the former arise the flat broad lateral twigs which serve as organs of assimilation[3].

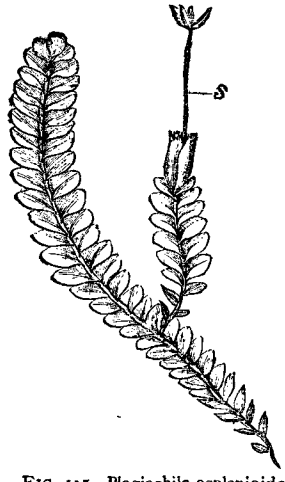

FIG. 115. Plagiochila asplenioides. Stem seen from above. The dorsal edge of each leaf is inserted lower down on the stem than the ventral edge. *S* sporogonium. Natural size. Lehrb.

In concluding this subject a few other relationships of configuration of Bryophyta upon which light has a directive influence may be cited:—

In the Bryophyta we frequently observe a displacement of the leaves from their original transverse insertion upon the shoot-axis in the bud to an oblique position, or, as in the extreme case of Schistostega, until the line of insertion coincides with the long axis of the stem itself. From my investigations I conclude that in many cases light has a direct influence upon this.

Plants of Jungermannia bicuspidata and of Plagiochila asplenioides (Fig. 115) placed in light of *very low intensity* developed positively heliotropic shoots in which frequently[4] the *transverse* position of the leaves was retained, the displacement being suppressed. In another Jungermannia with leaves having a more elongated insertion, there was displacement even in etiolated shoots. Schistostega occupies a somewhat peculiar position amongst the mosses, because its leaves are arranged in two longitudinal series on the vegetative stem (Fig. 25). In the bud an original many-rowed

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[1] Sachs, Über orthotrope und plagiotrope Pflanzenteile, in Arb. d. bot. Instituts in Würzburg, ii. p. 256; Id., Lectures on Physiology of Plants, p. 527.

[2] Goebel, in Ann. du Jardin botanique de Buitenzorg, vii.

[3] For more details on this point see Part II of this book.

[4] In Plagiochila particularly the phenomenon was partial.

position is observed, and by a peculiar displacement a bilateral formation is developed out of a radial one in the course of individual development[1]. The plant grows in places of slight illumination and this position of the leaves enables it to use them to the best advantage.

Is light then, as Hofmeister conjectured, directly concerned in the change of the leaf-position? I can answer this question in the affirmative on the basis of my prolonged cultures. At first it was assumed that the direction of the light was of importance, that unilateral illumination had to do with the displacement. Were this so, then a plant grown upon a klinostat with a vertical axis of rotation ought to have a radial leaf-position; but this is not the case. Plants in such circumstances are still bilateral[2]; although occasional torsion of the stem and other deviations from the normal occur, the chief result remains the same. On the other hand, plants of Schistostega grown in very low light-intensity retain their radial character; they become in these circumstances positively heliotropic, and a change of the leaf-position does not seem necessarily bound up with this. Under luxuriant cultivation, shoots which in their lower part are bilateral may become radial in their upper part (Fig. 116, right and left), because the newly laid down primordia are radial (Fig. 116, in the middle); the leaf-insertions are then often displaced towards the longitudinal axis, not however in two rows but equally all round. Between radial and bilateral constructions there are then all gradations. There is however, apart from torsion of the shoot-axis, a source of error to consider in this instance: the sexual shoots have leaves in a radial position.

FIG. 116. Schistostega osmundacea, after cultivation in feeble illumination. The shoots on the right and the left of the figure were grown at first in normal illumination and in their lower parts have normal construction, the upper portions which developed in feeble illumination are radial. The middle shoot was grown from the first in feeble illumination and its leaves are radially placed throughout, usually with an oblique insertion. This shoot had not concluded its growth and might have produced sexual organs had the experiment continued.

[1] See Fig. 26 and Part II of this book.

[2] Plants cultivated for long on the klinostat show disturbances which are especially expressed in reduction of the leaves.

In my cultivations the sexual organs were laid down in autumn, and therefore count was not taken of all these shoots. In the following summer I noticed, as I have said, an extraordinary number of shoots, which, without producing sexual organs, had closed their growth [1]. The leaves in the shoots grown in feeble light were much smaller than the others, and this appears in the figures.

Hofmeister has conjectured that Fissidens, another moss with distichously placed leaves, owes its leaf-position to the direct action of light. Here however the matter is somewhat different, because the bilaterality in the shoots growing in light is produced at the apex through a 'two-sided' apical cell, from which two rows of leaf-forming segments are cut off, and I have never succeeded in causing radial shoots to develop in Fissidens adantioides by cultivating it in feeble light [2]; even in darkness the shoots which appeared were distichous; and I therefore conclude that in Fissidens the transition from the radial to the bilateral structure has now become an inherited character, and is no longer a consequence of the direct influence of light.

The sporogonium of mosses shows in some cases a dependence upon light, which may be noted here, because it is connected with the behaviour of dorsiventral organs, upon the disposition of which light has a definite influence.

The capsules in the sporogonia of many mosses are radial, and either spherical or cylindrical in form, as, for example, in Sphagnum, Orthotrichum, Grimmia, the Phascaceae; but in others a more or less strongly marked dorsiventrality appears which, as I have shown [3], stands in evident connexion, in many cases at least, with the scattering of the spores. This dorsiventrality arises, so far as I have been able to determine, in the course of development even in the cases where it is most marked, for instance, in Buxbaumieae. The young sporogonium here is always radial, notwithstanding Wichura's [4] statement to the contrary, and the dorsiventral construction shows itself most strikingly in this—that the mouth of the capsule no longer falls in a straight line with the stalk, and the beak of the unopened capsule is thus placed obliquely to the shaded side in Buxbaumieae, Barbula subulata, and Catharinea undulata, to the illuminated side in Bryum argenteum. Whether the curvature would be entirely suppressed in capsules which were cultivated through the younger stages in light varying in its direction is unknown, so that the whole

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[1] All the shoots of Schistostega have limited growth.

[2] Hofmeister (Pflanzenzelle, p. 140) figures a plantlet of Fissidens bryoides upon which the lowermost three leaves—here laid down under ground—are tristichous whilst the upper leaves are distichous. This is a consequence of the apical cell being at first three-sided in this plant.

[3] Goebel, in Flora, lxxx (1895), p. 459, and lxxxii (1896), p. 480.

[4] Wichura, Beitr. zur Physiologie der Laubmoose, in Pringsh. Jahrb. ii. p. 193.

question still requires experimental investigation. The dorsiventrality of the capsule of the Buxbaumieae is the most striking. Diphyscium foliosum (Fig. 117), as well as the species of Buxbaumia, possesses an oblique capsule, one side of which is flat and the other convex, when seen in transverse section, and the former is the illuminated side. In young radial sporogonia of Diphyscium foliosum, which I cultivated in unilateral illumination, I found that the flattening always takes place on the illuminated side, which is here that part of the capsule-wall through whose movement (brought about by rain-drops) the discharge of the spores through the peristom-fringe is facilitated. In Fig. 117, which represents a longitudinal section through a sporogonium not yet quite ripe, but still possessing calyptra and operculum, the difference between the illuminated and the shaded side is quite evident; the sporogonium at a later stage is not so erect as is shown in the drawing. The flattening upon the illuminated side has also a relation to assimilation, seeing that the sporogonia during their development are able to assimilate by their chlorophyll-tissue, but in Diphyscium the relation to the scattering of the spores is the more important.

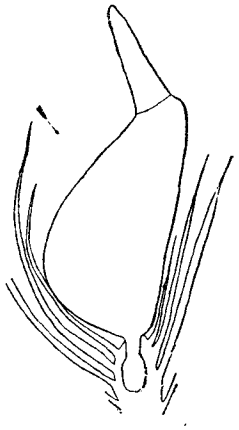

FIG. 117. Diphyscium foliosum. Longitudinal section of a stem bearing a sporogonium.

We must include a number of marine Algae amongst plants in which the position of the branches is determined by the influence of light. In Halopteris filicina, for example, the branching is commonly distichously alternate; radially branched examples however also occur. Berthold[1] has investigated experimentally the behaviour of Antithamnion cruciatum, one of the Florideae. He found that plants cultivated in the *horizontal position* had their 'leaves' laid down only in the horizontal plane, whereas on the positive heliotropic shoots they arose in all directions. Callithamnion corymbosum behaves in the same way. Fig. 43, of Antithamnion (Pterothamnion) Plumula, shows that its branching takes place normally in one plane, but occasionally there are found lateral twigs both on the upper and on the under side, although these are usually in a reduced condition. In other bilateral algae, the dorsiventrality is 'inherent,' that is to say, it is not caused by external factors.

In the regeneration of many Siphonieae[2] the directive influence of light is very apparent. The 'leaves' of Caulerpa are capable of producing

[1] Berthold, Beitr. zur Morphologie und Physiologie der Meeresalgen, in Pringsh. Jahrb. xiii. Many of the details in this paper are incomprehensible to me.

[2] Noll, Über den Einfluss der Lage auf die morphologische Ausbildung der Siphoneen, in Arb. d. bot. Instituts in Würzburg, iii (1888), p. 466.

new formations on both sides; if however the illumination be unilateral the new formations arise only upon the illuminated side of the 'leaves.' Similarly 'rhizomes' illuminated from below produce 'leaves' upon the side which previously formed 'roots'; dorsiventrality is reversible as in the prothalli of ferns [1].

2. QUALITATIVE INFLUENCE OF LIGHT.

We shall not consider in this place any of the phenomena that are grouped together as etiolation because these are more properly dealt with in physiological textbooks. The following subjects, of importance in organography, are treated of separately here only to enable us to present a general review of them; it will be understood that they frequently overlap:—

(*a*) Different developmental stages of one and the same plant are associated with light of different intensity, the earlier developmental stages claiming, that is to say being 'attuned' to, a less intensity of light than the later stages.

(*b*) The flattening and consequent increase of surface of organs containing chlorophyll in consequence of illumination.

(*c*) The influence of light in anisophylly.

(*d*) The change of function of homologous organs according as they grow in light or darkness.

(*e*) The influence of light upon the relationships of configuration of Fungi. This will be shortly referred to, facts not having weight in organography being omitted.

(*a*) DEVELOPMENTAL STAGES IN RELATION TO LIGHT.

When speaking of juvenile forms I have already mentioned examples of what I am now about to refer to here.

ALGAE.

The 'pro-embryo' of Batrachospermum [2] develops the Batrachospermum-plant only in bright illumination; in feeble light the plant remains stationary in the lowest stage of formation of organs, whilst the pro-embryo attains a luxuriant development. The same is the case in other Algae [3] whose germ-plants, if light is feeble, do not develop beyond the stage of the fixing disk or anchoring filaments; they form no erect thallus, but the fixing disk develops very strongly.

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[1] Regarding Bryopsis, see Noll, in Arb. d. bot. Instituts in Würzburg, iii (1888), p. 468.

[2] Sirodot, Les Batrachospermes, Paris, 1884.

[3] Berthold, Zur Morphologie und Physiologie der Meeresalgen, in Pringsh. Jahrb. xiii. p. 673.

BRYOPHYTA.

In the Bryophyta we have to deal with like phenomena. On the one hand the appearance of the individual moss-plant on its protonema is associated with the existence of a more intense light than is required for the luxuriant growth of the protonema itself[1]; and on the other hand the form of the protonema itself is influenced by light. Both conditions will be here spoken of together.

HEPATICAE. In many liverworts the germinating spore forms in the first instance a germ-tube which in the Marchantieae flattens out at its apex to a pluricellular germ-disk from which the young plantlet sprouts. In other forms, the germ-tube passes at its apex directly into the plant[2]. Germination takes place so far as it has been investigated only in the light. The germ-tubes are positively heliotropic in diffuse light, and Leitgeb has pointed out that their length depends upon the intensity of the light; in feeble light they are longer than they are in stronger light, and further, in feeble light there is laid down neither the primordium of a germ-disk nor of a leafy plant. I may mention here as an example the germination of Preissia commutata (see Fig. 118)[3]. The germination of the spore takes place in bright light in the manner shown in Fig. 118, *1*. A short germ-tube is produced, and out of its uppermost cell there proceeds a flat germ-disk at right angles to the direction of the light. This disk in many cases consists of two cells, in others of four. One[4] of these cells will become the apical cell of the young plantlet, which is at first very simple in structure, being composed of only one layer of cells, and it is only later that the characteristic structure of the thallus of

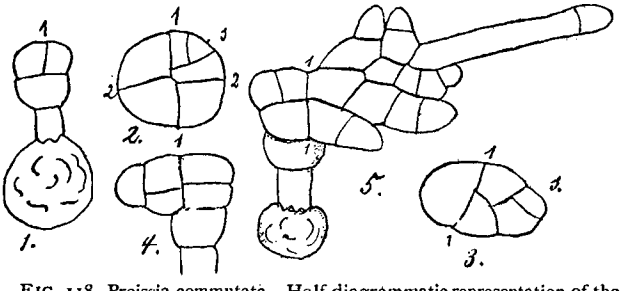

FIG. 118. Preissia commutata. Half diagrammatic representation of the germination of spores, partly from Hansel's figures. In *1* and *5* the spore is shown below. *1*, a germ-disc is produced at the end of a short germ-tube. *2* and *3*, two germ-disks seen from above; 1 1, the first segment-wall; 2 2, the second segment-wall; from one of the four quadrant cells the young plant usually proceeds, but as is shown in *3* the plant may develop from one of the cells resulting from division by the first segment-wall. *s* apical cell of young plant; this cell has developed again a germ-tube after forming five segments in *5*. *4*, germ-disk in optical cross-section with the primordium of a young plant on the left.

[1] There can be no doubt that the heliotropic movements also of the pro-embryo are 'attuned' to a less intense light.

[2] See Part II of this book.

[3] See Schostokawitsch, in Flora, lxxix (Ergänz.-Bd. 1894), p. 358.

[4] Leitgeb says the primordium of the plantlet arises in the most illuminated quadrant of the germ-disk in the Marchantieae; but as the disk is spread out at right angles to the light-rays all the quadrants should be equally illuminated. This is well seen in Preissia where the disk consists sometimes of only two cells.

Preissia appears. So long as this plantlet is in the simple juvenile stage, growing by means of a vegetative point with a 'two-sided' apical cell, it can be forced to revert to the formation of a germ-tube by bringing it into light of low intensity (Fig. 118, *5*). This germ-tube is able to produce a germ-disk in light of higher intensity, and again reversion can be induced. This process can be repeated at will. But whenever the young plant has reached the 'mature form' reversion to formation of germ-tubes is no longer possible. This reversion is really not different from what we have subsequently to consider in the chapter upon change of function caused by light[1], nor from what has been already mentioned—that formation of roots is favoured by want of light.

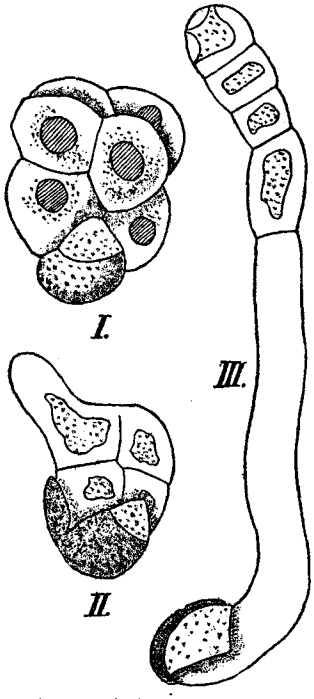

FIG. 119. Anthoceros. *I*, cell-mass produced in germination. *II*, cell-filament developing from the cell-mass. *III*, further stage of the cell-filament. After Leitgeb.

I have satisfied myself through the examination of Plagiochasma Aitoniana that the formation of its germ-tube cannot be hindered by light of very strong intensity, but the behaviour in germination of other liverworts is somewhat different and requires more accurate investigation. In Blasia pusilla, Anthoceros, Alicularia, and some other leafy Jungermannieae, either a germ-tube or a cell-body may arise, according to Grönland[2] and Leitgeb[3]. The germ-tube is produced according to Grönland only if the spores are sown very thickly, the cell-body is formed in Blasia when the spores lie scattered, and we may account for this by saying that external conditions, and after the analogy of other cases the intensity of the light, determine which kind of germination shall take place. As in Preissia too, the cell-body which develops in the germination of the spores of Blasia and Anthoceros may again form a tube which behaves like a germ-tube if it be placed in light of low intensity (see Fig. 119, *I–III*). That the formation of a germ-tube here is of as much advantage as the strong elongation of the axis of the seedling from a seed that is sown too deep, is quite evident—the germ-tube endeavours to reach the light. We can speak of the formation of germ-tubes then as an *adaptation* which in some liverworts has become inherited,

[1] See p. 255.

[2] Grönland, Mémoires sur la germination de quelques Hépatiques, in Ann. d. Sc. Nat., sér. 4, i.

[3] Leitgeb, Untersuchungen über die Lebermoose, i. p. 52, and ii. p. 67. Leitgeb conjectures that moisture is a determining factor upon the form of the pro-embryo; but light is certainly the predominating one.

that is to say, it appears first in the germination in all circumstances and is only dependent in its duration and development in length upon the light, whilst in others its first appearance is determined by light. The question whether the germ-tube represents a phylogenetically older stage does not concern us here.

MUSCI. In the mosses the phenomena are quite similar. Moss-buds appear upon the protonema only when the intensity of light is higher than that which is required for the normal growth of the protonema[1]. If the formation of buds does not take place the protonema may theoretically continue its growth to an unlimited extent. As has been previously stated the primordia of moss-buds may, up to a certain stage in their development, be induced to revert to the protonema-form. It is clear that it is of advantage to a moss that the primordia should only develop into moss-plants under conditions which offer to them a prospect of success. The construction of a moss-plant is of a higher character, especially in its capacity for assimilation, than is that of the protonema, and the formation of organs in the leafy moss-plant is, so far as we can judge from insufficient investigations, in a far greater degree dependent upon light than is the case amongst the Pteridophyta and Spermaphyta.

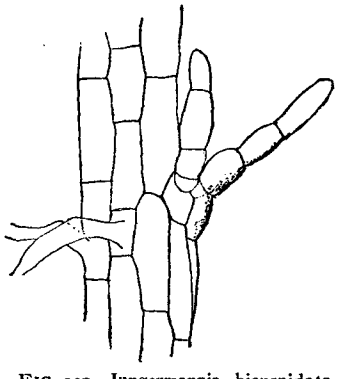

FIG. 120. Jungermannia bicuspidata. Portion of a stem grown in feeble light. To the right a leaf which consists of only some two cell-rows, whilst in normal illumination the leaf forms a cell-surface.

When etiolation takes place in the Bryophyta the leaf-formation is affected, the unfolding is often retarded, or the leaf is smaller than in plants grown in light; but in the cases which have been examined the outer differentiation is otherwise unaffected. Fig. 120 represents a leaf of a plant of Jungermannia bicuspidata which has been grown in feeble illumination and the normal construction is so greatly simplified thereby that it conforms with the leaves which appear in quite young plants. Similar cases may be found elsewhere.

PTERIDOPHYTA.

Regarding the sexual generation of the ferns we need only mention here that the formation of a cell-surface is associated with a greater light-intensity than is the formation of a germ-filament, and that for the development of sexual organs a high light-intensity is also required.

[1] Klebs, Über den Einfluss des Lichtes auf die Fortpflanzung der Gewächse, in Biolog. Centralblatt, 1893.

SPERMAPHYTA.

Vegetative organs.—In some cases it has been shown that the formation of the primary leaves[1] takes place in feebler light than does that of the succeeding leaves, and that in feeble illumination the plant may be caused to revert to the stage of primary leaves. This is the case in Sagittaria and in Campanula rotundifolia.

With regard to Sagittaria I have already spoken on page 172. Plants brought into feeble light formed only the strap-like primary leaves. The course of development was otherwise normal as was shown by the fact that the tubers for asexual propagation were formed. There can be no doubt that Sagittaria can be brought back to its primary stage by other influences; in nature this happens if the plant be in deep or rapidly flowing water.

Campanula rotundifolia, a typical land-plant[2], shows like relationships. It has two forms of leaves, rounded leaves and linear leaves, which are connected with one another by intermediate forms. The rounded leaves have a kidney-shaped lamina and a long stalk, and are the first leaves produced by the developing seedling at a time when it is growing amongst other plants and is therefore exposed to less intense light than it subsequently receives. These rounded leaves are then 'attuned,' so to speak, to light of low intensity. The internodes of the shoot-axis which bears them are short. The linear leaves have no stalks, or these are very short, and the blade is long; they stand upon that portion of the shoot which has elongated internodes and which subsequently in normal conditions ends with flowers. If the plant be cultivated in light of feeble intensity, but yet sufficient for nutrition and for the formation of primary leaves, it can be thrown back to the state in which it forms rounded leaves, even although it has already formed linear leaves (see Fig. 121). I may further remark here that, as my researches have shown, the seedlings in all circumstances form at first rounded leaves, even in very strong illumination. The spores of Funaria also under these conditions formed a protonema which was not less developed than usual.

Reproductive organs.—That the formation of reproductive organs is linked with the existence of a definite intensity of light follows indirectly from what has been said. In the mosses they arise, as we know, only upon the leafy stem, and in Campanula and Sagittaria formation of flowers is preceded by the 'higher' form of leaf.

Sachs was the first who made an accurate investigation of the dependence of *formation of flower* upon light. A superficial consideration

[1] See the Third Section.

[2] Goebel, Über den Einfluss des Lichtes, &c., ii. Die Abhängigkeit der Blattform von Campanula rotundifolia von der Lichtintensität, in Flora, lxxxii (1896), p. 1.

might lead us to the conclusion that formation of flower is independent of light, for we see bulbs of hyacinth, tulip, and other plants, bringing forth their flowers in darkness, and even on completely etiolated seedlings of Phaseolus vulgaris, Vicia Faba, and Cucurbita Pepo we can occasionally prove the beginning of the formation of flower[1]. In the first set of these cases however we have simply to do with the unfolding of the flower-buds already laid down in the bulbs, and in the second we are dealing with seeds which are rich in reserve-materials the most favourable for formation of flower. If we place in darkness plants of, say, Brassica, Tropaeolum, Papaver, Cucurbita, or others, already provided with flower-buds, these buds will not unfold if the plants have been withdrawn from the light in too early youth; older buds unfold themselves but often less completely, and in Tropaeolum there appears a kind of cleistogamy inasmuch as some of the flowers which do not unfold show rudiments of seeds. On the other hand the etiolated plants

FIG. 121. Campanula rotundifolia. Shoot with linear leaves which was placed in conditions of feeble illumination. The flower-buds, *K*, which were already laid down have been arrested. A lateral shoot, *A*, has developed, bearing rounded leaves; such shoots are never produced under normal conditions. If flower-buds had not been laid down the chief shoot itself might have produced rounded leaves *after* the linear ones under the conditions of feeble illumination.

[1] Sachs, Gesammelte Abhandlungen, i. p. 207.

form vegetative shoot-parts, whose mass should be sufficient for the formation of new flowers if it was merely a question of *mass* of formative substance and not of its special nature. Sachs assumed the existence of a special 'flower-forming material' which is produced in the leaves and only under the influence of light. This can however be transferred to parts of plants placed in the dark, as is proved in nature by the development of flower-buds on subterranean bulbs and tubers, and experimentally by leading a portion of a shoot into a dark chamber whilst a number of the leaves remain in light—on the new shoots formed in darkness numerous flowers arise; eventually abnormalities appear, and these may be accounted for by the fact that the path of the flower-forming material from the leaves is always getting longer.

Sachs[1] was led by subsequent experiments with Tropaeolum to the conclusion that the ultra violet rays are specially needed for formation of flower. Plants were cultivated behind a screen of a solution of sulphate of quinine and only in exceptional circumstances did the formation of a single flower take place; usually the formation of flower was entirely suppressed. The plants themselves, it may be remarked, were only slightly etiolated but otherwise normal. The question of the significance of the ultra violet rays requires however more extended investigation[2]. It is certain that the intensity of light plays an important part in the formation of flower, and that for this a much higher intensity of light is required than suffices for the formation of vegetative organs. To this conclusion the researches of Vöchting[3] led him. He says:—'In order that plants may form flower in a normal way the illumination must not sink below a certain amount which is very unequal in different species. Shade-plants and sun-plants require different degrees of illumination for the performance of the same functions. . . . Impatiens parviflora, for example, a shade-plant, produces complete flowers under illumination which would scarcely enable Malva vulgaris, a sun-plant, to form buds. . . . If the illumination is allowed to sink below the required amount, the size of the whole flower, or of its individual parts, is diminished and with decreasing illumination a stage is reached at which formation of flower entirely ceases. In many species the stage at which complete cessation

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[1] Sachs, Über die Wirkung der ultravioletten Strahlen auf die Blütenbildung. Gesammelte Abhandlungen, p. 293.

[2] C. de Candolle has published in 'Étude de l'action des rayons ultra-violets sur la formation des fleurs,' in Archives des Sciences phys. et natur. xxviii (1892), the result of a repetition of Sachs' experiments. He found no flowers in two plants after cultivation behind a screen of solution of sulphate of quinine for seventy-one days; thirty-three flower-buds in two plants grown behind an equally thick screen of water; behind a screen of aesculin flowers were formed in Lobelia Erinus, but in smaller numbers than behind water.

[3] Vöchting, Über den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüten, in Pringsh. Jahrb. xxv. p. 149.

of production of flower takes place is preceded by one in which whilst the buds are laid down they die off at an early period of youth. The intensity of illumination which marks this lower limit is again very different for the different species.' The influence of diminution in the degree of illumination shows itself in the first instance in the corolla. In some species like Melandrium album, M. rubrum, and Silene noctiflora, it remains in its early bud-condition, whilst the sepals, stamens, and carpels attain their normal size; in others, for example Mimulus Tilingii, all the parts of the flower diminish in size, but the stamens and carpels show themselves less dependent upon light than the corolla. In some species when the illumination is deficient the flowers are always open, even although there be a reduction in size of the corolla or of the whole flower, whilst in others the flowers remain closed[1]; this especially occurs in forms which like Stellaria media have a tendency to cleistogamy, or which produce special cleistogamic flowers like Linaria spuria. In such cases it is possible to produce by regulation of the illumination either flowers which open, that is to say are chasmogamic, or closed flowers, that is to say cleistogamic ones; this is not however the case in Viola. It cannot well be doubted, and I may cite as ground for this a fact which I have published elsewhere[2], that in uniform conditions of light other factors may evoke the production of cleistogamic flowers in plants which usually produce them. We may also assume that the minimum of any factor, for instance of temperature, for the formation of flower does not usually coincide with that for the vegetative organs. We already know from what has been said on page 212 that plants in which formation of flower is hindered by insufficient intensity of light very often exhibit luxuriant formation of vegetative shoots.

Further investigation is required regarding the influence of light upon the formation of sporangia in the Pteridophyta. I am disposed to think that relationships analogous with those observed in connexion with formation of flower exist there[3].

(*b*) Flattening and Increase of Surface of Organs in relation to Light.

It is characteristic of the condition about which we have now to speak that it seems to occur only in organs containing chlorophyll. When we observe a marked development of the surface in such organs, most conspicuously in leaves, its advantage in assimilation which is dependent upon light requires no demonstration. I have already briefly mentioned on page 241 a case in point—the germ-tubes of the prothalli of ferns only

[1] See what is said about Tropaeolum on p. 244.

[2] Goebel, Pflanzenbiologische Schilderungen, ii. p. 363.

[3] See what I have said on this subject in Flora, 1895, p. 116.

become cell-surfaces in light of high intensity, whilst they continue to grow as tubes if the illumination is feeble. Like phenomena are found in a number of plants from the most different groups of the Plant Kingdom. But we also observe the phenomena of flattening of the illuminated side in organs where we can discover no utilitarian explanation, as, for example, in the shoot-axis of plagiotropous mosses (Fig. 113), in the climbing stems of some monocotyledonous plants; in other cases however the use of the flattening and of the increase of surface (which is not always a necessary consequence) is quite evident. The roots of some monocotyledonous and dicotyledonous plants furnish instructive illustrations.

Normal radial roots without chlorophyll are buried in the soil. But the roots of some, although not all, plants have the capacity of becoming green when exposed to the light, and this happens regularly in the aerial roots of many Orchideae, and in Podostemaceae which possess roots. The roots containing chlorophyll in both these families have often a form different from that of the ordinary root; they acquire a dorsiventral construction which in the case of the orchids is exhibited particularly in the structure of the velamen, and in addition the roots often become flattened and to such an extent that they are quite leaf-like[1]. When this flattening takes place in roots lying on a substratum, that upon the side of the root touching the substratum must be distinguished from that on the side directed to the light. The former is brought about by the firm fixing of the root on its substratum, such as stems of trees, stones[2]; the latter, so far as there is a difference between the illuminated and shaded side, is at least in many cases caused by the light[3]. We see this in Sarcanthus rostratus and S. Parishii, Epidendrum nocturnum, and Phalaenopsis amabilis. In the last-named plant those of its roots which are buried in the substratum are cylindric and radial, whilst those growing in light are flattened on the illuminated side and the velamen there shows a structure affording a greater protection against transpiration than is found upon the shaded side. In Angraecum fasciola the dorsiventral aerial roots are not the result of the direct influence of light, for they develop in this form even in darkness.

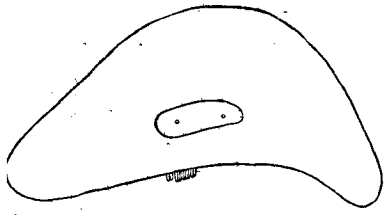

FIG. 122. Oenone leptophylla, one of the Podostemaceae. Transverse section of the dorsiventral green root. The ventral side which is fastened to the substratum by many hairs, some of which are indicated, is flattened, but the dorsal side is also somewhat flattened. The vascular bundle system is excentric.

[1] The name Taeniophyllum tells that Blume mistook the flat green roots in this genus for leaves. See my 'Pflanzenbiologische Schilderungen,' i. p. 194.

[2] See what is said about shoots on page 90.

[3] Janczewski, Organisation dorsiventrale dans les racines des Orchidées, in Ann. d. Sc. Nat., Sér. 7, xii (1885); Goebel, Pflanzenbiologische Schilderungen, i. p. 197, and ii. p. 351.

The roots of Podostemaceae[1] which are spread out upon stones show an analogous behaviour. In Fig. 122 a tranverse section is shown of their dorsiventral configuration, and the flattening on both sides is evident. This flattening reaches an uncommon degree in Dicraea algaeformis and in Hydrobryum[2]. We have no experimental investigations up till now upon these cases, yet we may assume that at least in many of them the increase in surface is the result of the direct influence of light, and we shall probably not be wrong if we assume that in other cases the condition has 'become inherited.'

In most Cacteae the shoot-axes have become transformed into organs of assimilation and storage concurrently with an arrest of their leaves. These shoots often exhibit increase of surface which may be brought about in different ways[3]. In many species of Opuntia the shoot-axes are strongly flattened; they develop out of a radial vegetative point and they show their radial origin in their possession of tufts of spines on all sides. It has now been established[4] that in some forms, for example Opuntia leucotricha (Fig. 123), the flattening does

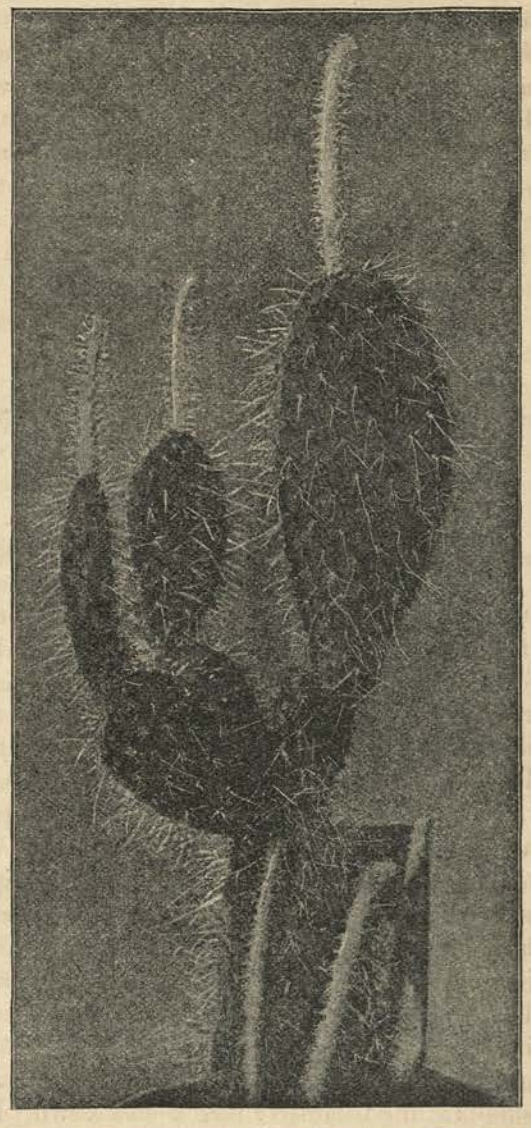

FIG. 123. Opuntia leucotricha. Plant which has developed shoots in darkness. These shoots are cylindric, not flattened as are the normal shoots produced in the light. The internodes of the shoots formed in darkness are not elongated as is commonly the case in etiolated shoots.

[1] For the biological relationships of this remarkable group see my 'Pflanzenbiologische Schilderungen,' ii. p. 2.

[2] See the chapter upon the Root in Part II of this book.

[3] Goebel, Pflanzenbiologische Schilderungen, i.

[4] Goebel, Über die Einwirkung des Lichtes auf Kakteen und andere Pflanzen, in Flora, 1895, p. 96. Sachs' work is referred to in this paper.

not take place in the absence of light, the etiolated shoots grow then cylindrically. From occasional observation we know that the etiolated shoots in some other species are flat but much smaller than normal, and if such shoots be placed in the light the newly formed parts have the normal flat construction and, according to Sachs, if the shoots be exposed to intense illumination from one side the flat sides take a position so that the light falls perpendicularly upon them. Those species of Opuntia are very

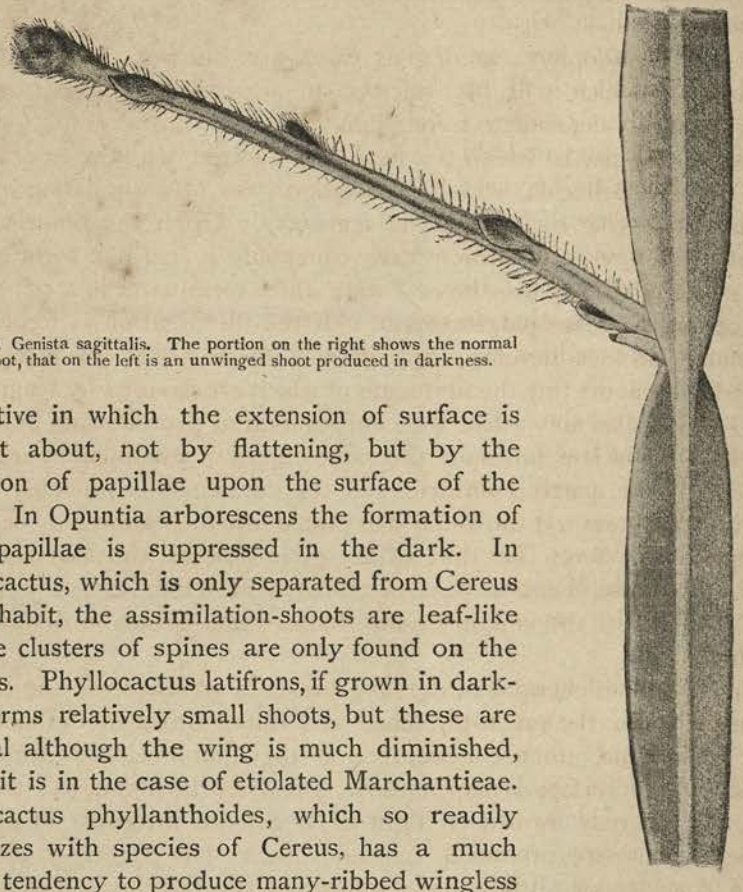

FIG. 124. Genista sagittalis. The portion on the right shows the normal winged shoot, that on the left is an unwinged shoot produced in darkness.

instructive in which the extension of surface is brought about, not by flattening, but by the formation of papillae upon the surface of the stem. In Opuntia arborescens the formation of these papillae is suppressed in the dark. In Phyllocactus, which is only separated from Cereus by its habit, the assimilation-shoots are leaf-like and the clusters of spines are only found on the margins. Phyllocactus latifrons, if grown in darkness, forms relatively small shoots, but these are bilateral although the wing is much diminished, just as it is in the case of etiolated Marchantieae. Phyllocactus phyllanthoides, which so readily hybridizes with species of Cereus, has a much greater tendency to produce many-ribbed wingless shoots; in darkness it forms shoots with many rows of clusters of spines; if it is placed in illumination the formation of wings begins and then there is reduction of the rows of spines to two. It is impossible here to go further into details[1].

The influence of light which I have just depicted is by no means restricted to the Cacteae. Fig. 124 shows a portion of a shoot of Genista

[1] See the literature cited by Vöchting, Über die Bedeutung des Lichtes für die Gestaltung blattförmiger Kakteen, in Pringsh. Jahrb. xxvi. p. 438.

sagittalis. The leaves are greatly reduced, the shoot-axis broadly winged, as appears in the portion of the figure to the right. To the left is shown a lateral shoot which has developed in darkness and in it the wing which starts from the leaf-base appears as only a small rib, and the whole shoot has quite a different look because the increase in surface has not taken place. All plants however do not exhibit a like reaction. The leaf-like twigs of Ruscus aculeatus, for example, if etiolated through growth in darkness, are smaller than the normal ones but otherwise agree with them in form.

Amongst Pteridophyta analogous cases are known. In Lycopodium complanatum, which will be referred to again below, the growth in surface extent is dependent upon light.

With the Cacteae to which we have just referred, we may associate the moss Tetraphis pellucida, which possesses organs of assimilation upon its protonema behaving exactly in the same way. Upon the branched cell-filaments structures arise which have commonly a leaf-like form and are organs of assimilation; they have a stalk which terminates in a cell-surface. These cell-surfaces are plagiotropous. If the illumination is feeble these cell-surfaces do not develop, but instead there arises an erect richly branched protonema-tuft the filaments of which are divided by longitudinal walls[1]. Light also may affect the configuration of protonemata in another way. In Diphyscium foliosum the same organs of assimilation are partly flat and leaf-like, partly cylindric, and the difference is probably due to light; in Sphagnum too the usual flat protonema-formation may occasionally appear in a form like that of the germ-disk of the Marchantieae[2]. We may here also mention that in etiolated Marchantieae, as well as in Blyttia, and others, the shoots of the thallus when grown in darkness are quite small.

The large peripheral bladder-like branches which serve the purpose of assimilation in the much-branched and tufted tubes of Codium[3], one of the Siphonieae, are not developed if the illumination is feeble and thus increase of surface is suppressed. Similarly in Caulerpa[4] the leaf-like organs are only formed in light of a definite intensity, in darkness cylindric organs are produced instead. Sachs has rightly conjectured that the considerable surface development of the vegetative body of the lichens, as compared with that of fungi, is caused by their containing chlorophyll which brings about a different reaction towards the stimulus of light.

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[1] Correns, Über die Brutkörper der Georgia pellucida und der Laubmoose überhaupt, in Ber. d. deutsch. bot. Gesellsch. xiii. p. 426.

[2] See Part II of this book.

[3] Berthold, Morphologie und Physiologie der Meeresalgen, in Pringsh. Jahrb. xiii.

[4] Klemm, Über Caulerpa prolifera, in Flora, 1893, p. 460.

The phenomena of anisophylly are in the main, as we have already seen, connected with the provision of a favourable surface for assimilation, and we have therefore next to speak of it in its dependence upon external factors, so far as we know them.

(*c*) Anisophylly in relation to Light.

In the second section, I have discussed the features of anisophylly in detail, and shown that, as Herbert Spencer first recognized, the advantage of anisophylly lies in the favourable surface for assimilation it provides. This does not mean that light must be the determining factor for the occurrence of anisophylly; but I showed some years ago[1], in examples from the silver fir, that anisophylly is strongly influenced by light. The plagiotropous lateral shoots of this tree are, as is well known, dorsiventral. 'This appears both in the position and in the construction of the needle-leaves. The former varies . . . . according to the illumination; in the lower twigs of trees standing in close wood or of young examples growing in the shade of older ones, the whole needle-leaves are "pectinated"[2], through twisting of the leaf-base, and have their green upper side turned upwards to the light, their white under side turned downwards away from the light. Such shoots behave then like a thallus of Marchantia—they possess an upper side constructed differently from the under side. The influence of light shows itself also in the relationship in size of the leaves—the leaves on the upper side are distinctly shorter than those on the under side. The following measurements of length of leaf will illustrate this:—

1. Leaf upon the under side of a twig: this leaf turned its upper side upwards without torsion—16 mm.

2. Next following leaf approaching the flank of the dorsal side —10·5 mm.

3. Next leaf inserted entirely upon the upper side—8 mm.

4. Next leaf inserted entirely upon the under side—18 mm.

There is thus a difference amounting to more than double their length between the shortest and the longest leaves, and the smallest are those which stand furthest apart upon the upper side, the largest are those standing upon the shaded side but which really assume a lateral position on the shoot. The leaves on the erect chief shoot are on the other hand all equal in size, and compared with them those which stand upon the illuminated side of the twigs have suffered a restriction in their development. In strong illumination in the open the needles on the twigs are

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[1] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, p. 146. See also Goebel, Über einige Fälle von habitueller Anisophyllie in Botan. Zeitung, 1880, p. 839, where I deal with the relationship of light to plagiotropous growth.

[2] The character of the foliage of the silver fir expressed in the specific name—Abies pectinata.

not pectinated; their surface is then not placed at right angles to the incident light rays, but they are all more or less upright in the direction of the dorsal surface of the shoot, and those which stand upon the dorsal surface itself show in consequence not infrequently wax-striae upon their upper side, but these are not so strongly developed as are those upon their under side. Anisophylly then appears here also, but it is not so striking as in the first-mentioned case, and without measurement is scarcely recognizable. Some examples of measurements of needles chosen at random may be given, *a* being dorsally placed ones, and *b* ventrally placed ones,—

a	*b*
19 mm.	22 mm.
16 mm.	21 mm.

Sometimes the differences are greater, sometimes they are smaller. The relations of the dorsiventrality to illumination are also here instructive; the smallness of the dorsally placed needles is perhaps so far of benefit as thereby an overlapping of the laterally placed ones is avoided.'

We see that in strongly illuminated twigs anisophylly almost disappears, in feebly illuminated ones, on the other hand, it is strongly marked, and I particularly direct attention to this because the dorsiventrality here has been considered by many authors as an effect of gravity. Kny[1], for example, takes this view on account of the following investigation:—'Many twigs of Abies pectinata were firmly fastened in an inverted position at the beginning of November, 1871. As these unfolded their buds in the spring of 1872 without undergoing lateral torsion the horizontal position of the leaves underwent a change in correspondence with their new direction so that the dorsal side was turned upwards and the ventral side was turned downwards; on the other hand the anisophylly was retained in the same sense as it would have been in the normal position, that is to say, the upper leaves were the longer, the under leaves the shorter. The relationship of the longest to the shortest leaves was only slightly modified. It was not until the spring of 1873, quite a year and a half after the beginning of the experiment, that the influence of the new direction was undoubtedly evident in the proportional development of the leaves, and showed itself in this, that on the new shoots which were laid down by the mother-shoot in succession corresponding with its inverted position the anisophylly exhibited inversion in correspondence therewith.' This experiment shows clearly that the anisophylly is already determined in the bud. I have proved the same in the buds of Aesculus Hippocastanum[2], which develop anisophyllous shoots even

[1] Kny, Über die Bedeutung der Florideen in morphologischer und histologischer Beziehung und den Einfluss der Schwerkraft auf die Coniferenblätter, in Botan. Zeitung, 1873, p. 433.

[2] Goebel, Über einige Fälle von habitueller Anisophyllie, in Botan. Zeitung, 1880, p. 840.

when these shoot out in the most different directions and also when they appear in the dark. In Kny's experiment the influence of light was not excluded and the facts which have been stated above show that light must be considered essential for anisophylly. It is probable also that correlation plays a part. The lateral and under leaves of a twig of silver fir can reach their 'fixed light-position' quicker than do those of the upper side which have to undergo a strong torsion. It is evident also that less plastic material will flow towards a strongly shaded branch than to one strongly illuminated, and as a matter of fact the total mass of the leaves in the two is very different. If we now assume that shaded leaves are hindered in their growth [1], this retardation must be more felt in the upper leaves than in the under which can draw to themselves more rapidly the available material, because their horizontal position enables them to use earlier the available light. Gravity naturally acts equally in both cases; it is however unable to bring about a conspicuous anisophylly.

FIG. 125. Lycopodium complanatum. Shoot which has pushed out in darkness; only the chief axis of this relatively lateral shoot has pushed out, and the portion so developed has a radial construction. Magnified.

Another case in which anisophylly is caused directly by light is that of Lycopodium complanatum (Fig. 125). In autumn I placed in darkness the aerial parts of many plants of this species whilst they grew in their natural localities by turning a pot over them. *The parts developed the next year were radial.* We have already seen on

[1] Weisse found that in shaded leaves of Acer platanoides the growth of the lamina and stalk suffered diminution. See Weisse, Zur Kenntniss der Anisophyllie von Acer platanoides, in Ber. d. deutsch. bot. Gesellsch. xiii. p. 379; also Wiesner, Photometrische Untersuchungen auf pflanzenphysiologischem Gebiete, in Sitzungsb. d. Wiener Akad. d. Wiss. cii (1893), p. 291.

page 102 that the anisophylly is here very peculiar and of different strength on shoots of different orders. The lateral shoots of the last order, which are mostly flattened and provided with only four rows of leaves, do not generally shoot out in darkness[1] although this takes place in the case of the relative chief axis which is equally strongly dorsiventral and anisophyllous. On the shoot which is represented in Fig. 125, for example, the lateral leaves had the characteristic keel upon the back, and two leaf-rows were found upon both the upper and the under side, and they were constructed differently one from the other in the manner already described; the transverse section of the shoot-axis depicted on the left of Fig. 126 shows that upon the illuminated side the leaf-cushion was more pronounced than it was upon the shaded side. The shoots developed in darkness however had *entirely lost the anisophylly;* the leaves were all developed alike, there was no trace of formation of keel on the lateral leaves, there was only a slight flattening of the shoot-axis observable (see the representation on the right in Fig. 126); the branching of the shoot also no longer took

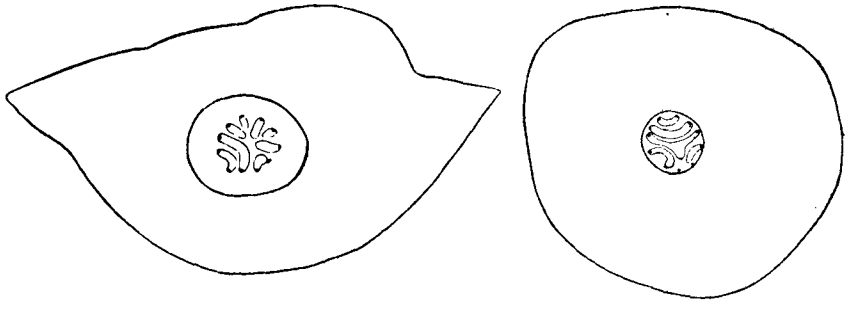

FIG. 126. Lycopodium complanatum. Two cross-sections through the same shoot. That on the left from a portion growing in light, that on the right from a portion growing in the dark.

place in *one* plane and it no longer formed the leaf-like lateral shoots with limited growth, in short this shoot behaved essentially like an underground rhizome. Dorsiventrality and anisophylly were directly induced by the light.

In other cases, for instance those of habitual anisophylly described on page 109, the anisophylly is retained even in etiolated shoots, for example, in Goldfussia anisophylla amongst others. In shoots of this species growing erect the anisophylly is modified but not destroyed, and it may originally have been brought about here in relationship to light.

[1] The lateral axes in the plagiotropous shoot-system of many mosses also do not develop in light of feeble intensity.

The facts recorded of Goldfussia[1] (Fig. 127) have led me to the view that internal relationships of symmetry have also to do with the anisophylly—the position of the lateral shoots to the chief shoot for example; and this is an opinion at which Wiesner[2] has also arrived after special study of the problem of the furtherance of the outer side of the lateral shoots. I cannot however agree with Wiesner that it is the strong influence of relative position to the mother-shoot upon the unequal leaf-development that brings it about that—'If strong stems provided with axillary shoot-primordia of Urtica dioica or Scrophularia officinalis come to be horizontal there are developed on the sides of these stems axillary shoots with strong anisophylly on which the outer leaves, that is those turned away from the mother-axis, are more developed than the inner,

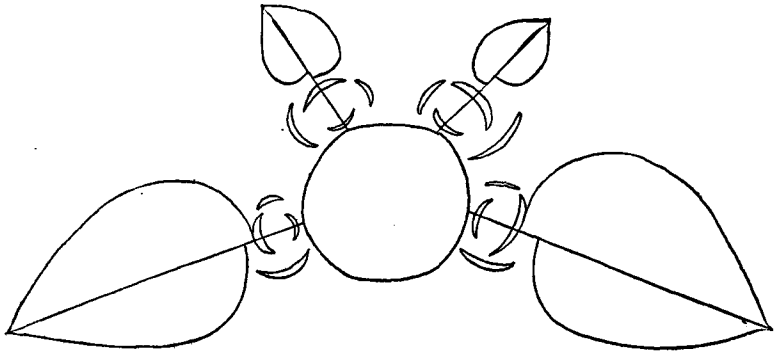

FIG. 127. Goldfussia glomerata. Scheme of the phyllotaxy and leaf-symmetry. The leaves stand at first in decussate pairs, but are subsequently displaced to the position represented.

that is those turned towards the mother-axis'; there may have been here, so long as the shoot was still vertical, an 'induction' of the bud which only found expression in the horizontal position.

In conclusion I must say a word about an experiment of Frank[3]. He inverted a horizontal twig of Acer platanoides when its terminal bud was so far opened that two pairs of leaves were visible. The first pair of leaves in spite of the altered position retained the primarily induced differentiation[4]; the second pair did so only at the beginning, later the leaf now lying undermost surpassed the upper; and in the third pair this was the case from the beginning. Light however was here not

[1] See what I have said about Centradenia grandiflora in Botan. Zeitung, 1880, p. 840.

[2] Wiesner, Anisomorphie der Pflanze, in Sitzungsber. d. Wiener Akad. d. Wissensch. ci., Abt. I (1892), p. 701.

[3] Frank, Über die Einwirkung der Gravitation auf das Wachsthum einiger Pflanzenteile, in Botan. Zeitung, 1868, p. 873.

[4] Weiss confirmed this by experimental growths on the klinostat, but added nothing new to what I had already proved in the case of Aesculus.

excluded, and Frank is hardly warranted in his conclusion from this experiment that the development of the under leaves to a greater extent than the upper ones on the shoots of Acer obtusatum produced by buds in darkness is an effect of gravity, because the anisophylly may be already induced in the bud, as I have shown above to be the case in Aesculus and Abies. In shoots of Abies canadensis the length attained by the upper leaves in light was about 4·7 mm., that by the under leaves was 12 mm.; in the natural position when developed in the dark they were respectively 6·2 mm. and 11·6 mm.; in the inverted position in the dark they were 7·2 mm. and 10·3 mm. From these figures Frank concluded that light acted as well as gravity upon the anisophylly in this case.

From what has been said it will be gathered that anisophylly is a complex phenomenon associated with different factors, but that everywhere it may be induced by definite, chiefly external, factors. These can directly influence the configuration, for example, in Abies pectinata and Lycopodium Chamaecyparissus, or impress upon the vegetative point of the bud definite peculiarities[1], or the 'induction' is, as in the case of habitually anisophyllous plants, a permanent one. One may also assume such an induction for those cases in which anisophylly appears to depend entirely upon the position of the lateral shoots in relation to the mother-axis. Further investigations are required for the full explanation of the question—investigations which must specially take into consideration the induction, probably appearing at a very early time, in the vegetative point of lateral shoots.

Kolderup-Rosenvinge[2] has found in Centradenia floribunda that in shoots fixed horizontally in an inverted position the anisophylly is inverted, that is to say, the larger leaves stand upon the side which was formerly uppermost. It is a fact that the anisophylly of this plant is very markedly influenced by the position of the shoot to the horizontal, and hence vertically growing shoots hardly exhibit it at all, whilst the horizontal ones do so in considerable amount. The experiments upon inversion which have been mentioned do not however prove that gravity is the critical factor in anisophylly, inasmuch as light may likewise influence the shoot differently in the horizontal position and in the vertical.

(*d*) Change of Function through Light.

The cases of the qualitative influence of light upon the formation of organs which have now to be dealt with cannot be sharply separated of course from those which have just been referred to, but it is interesting to deal with them specially.

[1] According to Frank's experiment they appear to act chiefly on the earliest stages of the primordia of the leaves.

[2] Kolderup-Rosenvinge, L'Organisation polaire et dorsiventrale des Plantes, in Revue générale de Botanique, i. p. 130.

The configuration of underground organs removed from the light differs usually considerably from that of homologous organs which are exposed to the light[1]. Thus rhizomes and stolons have scale-like cataphylls instead of foliage-leaves. The difference does not always depend directly upon light; but this is the case in Circaea[2]. Its seedling plant at first forms only one aerial shoot; in the axil of the lowermost foliage-leaves shoots arise which bend towards the earth, and upon these are developed at first foliage-leaves, which apparently in conformity with the inclined growth of the axis are smaller than those of the orthotropous shoot. As soon as the shoots enter the soil, they form scale-leaves instead of the foliage-leaves. But if one of these stolons be allowed to grow permanently with access to light, for example, in an illuminated water-culture, it forms instead of the scale-leaves small foliage-leaves, which do not lie close upon the axis, like the scale-leaves, but stand out from it, and thus exhibit a character which is associated with the possession of chlorophyll[3].

The stolons of the Hieracia behave in like manner, whilst those of Adoxa moschatellina form scale-leaves even under illumination.

The Algae especially furnish similar examples. Oedocladium protonema[4] is an alga living on land and having aerial much-branched green threads and subterranean thin sparingly-branched colourless 'roots.' If the latter be exposed to the light, they become green and are transformed into normal short-membered aerial twigs. On the other hand, on plants from which the 'roots' have been removed, new 'roots' arise in a short time, which are distinguished by their sparingly green colour and their negative heliotropism. Sometimes these are new formations, sometimes they proceed out of the apex of green twigs, from which I conjecture that relationships to light are critical. Berthold[5] has observed the following in marine Algae: 'If one brings specimens of different filamentous Algae, for example, Callithamnion, Bryopsis, Ectocarpus, from the sea into a culture-vessel in feeble illumination, the apices immediately grow out into rhizoid-like threads'; and Noll[6] has been able, in specimens of Bryopsis planted in an inverted position, to cause the short green twigs, even the apex of the plant itself, to develop into rhizoids, which are otherwise only formed at the basal end of the plant. Here however the condition of the

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[1] This of course is entirely apart from such differences as absence of chlorophyll.

[2] Goebel, Beitr. zur Morphologie und Physiologie des Blattes, in Botan. Zeitung, 1880, p. 794.

[3] Orthotropous shoots of Circaea do not produce scale-leaves in the dark, but etiolated foliage-leaves, and the shoots referred to in the text have evidently a definite peculiarity which determines their reaction in the way described.

[4] E. Stahl, Oedocladium protonema, eine neue Oedogoniaceengattung, in Pringsh. Jahrb. xxiii.

[5] Berthold, Morphologie und Physiologie der Meeresalgen, in Pringsh. Jahrb. xiii. p. 673.

[6] Noll, Über den Einfluss der Lage auf die morphologische Ausbildung einiger Siphoneen, in Arb. d. bot. Instituts in Würzburg, iii. p. 466.

plant itself has some bearing—the points of strong growing shoots will not become rhizoids, but bend in a negatively geotropic manner and continue their growth as organs of assimilation.

These last cases recall the fact stated above, that in the higher plants failure of light or feeble illumination is favourable to the formation of roots; in cases where the differentiation of the organs is not yet a sharp one, such illumination may result in the direct transformation of an organ of assimilation into a root or rhizoid.

(*e*) Influence of Light upon the Relationships of Configuration of the Fungi.

The formation of organs in dicotyledonous parasites containing no chlorophyll, for example, Orobancheae, Lathraea, Balanophoreae, may be accomplished in the absence of light even to the formation of flower. There is indeed but little room for doubt that the 'flower-forming material' of the parasites is formed for them by the host-plant. It would be of interest were this to be proved experimentally, and the annual species of Orobanche form specially favourable subjects for the investigation. Is the formation of their flower dependent upon the same factors as is that of the host-plant? It is quite possible that no such dependence exists, as in many plants the course of development is quite independent of light, whilst in others it is strongly influenced by it. It is well known that Agaricus campestris is produced in forcing houses in more or less complete absence from light, and that the Hypogaeae, which are partly Basidiomycetes, partly Ascomycetes, in like manner complete their whole development in darkness. Similarly Basidiobolus ranarum[1] forms its asexual organs (gonidia), as well as its sexual organs, equally well whether it be in light or in darkness.

We must first of all consider the *directive* influence of light.

In Polyporus fomentarius and Daedalea quercina, which live upon trees, the spore-forming hymenium of the fructifications is found normally upon their under side—that turned away from the light. If the block upon which the fungus grows be turned upside down[2], hymenium begins to be formed upon what was previously the uppermost side, whilst the hymenium of the previously under side, now exposed to the light, gradually dies off. There can be no doubt that the position of the hymenium upon the under side, which in the fructifications of other Hymenomycetes is a consequence of 'inner' causes, is of importance for the distribution of the spores, because the rain cannot affect them there, and the heliotropic movement exhibited

[1] Raciborski, in Flora, lxxxii (1896), p. 117.

[2] St. Schulzer v. Müggenburg, in Flora, 1878, p. 122. The effect of gravity is not considered in this research.

by the fructifications of many fungi is no doubt connected with distribution of spores also. These heliotropic movements influence, in some cases, the form of the fructification.

It is possible by changing the direction of the influence of light to cause the neck of Sordaria fimiseda[1] to assume any position desired, even to give it a spiral twist, because it turns itself always to the light; the fructifications of Ascobolus and Peziza likewise turn themselves to the light, so that their disk receives the rays at a right angle.

The colour and consistence of the fructifications of many Sphaeriaceae[2], as well as the length which their neck below its opening reaches, are dependent upon light. In Sphaeria velata, for example, the neck normally attains a length of 1 mm., but if light be excluded it may reach as much as 5 mm. This is not the place to discuss the heliotropic phenomena of Fungi, but it is of interest for us to note that in many the formation of the sporophore depends on light, whilst the mycelium is not influenced by light[3]. Thus in Pilobolus microsporus the formation of sporangia is suppressed in darkness, whilst their stalks are laid down but are puny and slender. The influence of light for a few hours suffices to bring about the changes which lead to the formation of sporangia. Sphaerobolus stellatus also remains completely sterile in the dark. Many Hymenomycetes lay down their fructifications in darkness, but these grow abnormal. Schröter found the sporophore of Stereum sanguinolentum in coal mines had only seldom the form of spread-out plates or half caps, which is the normal one; the whole sporophore was usually broken up into a great number of coral-like spreading branches, forming broad ridges and spikes hanging from the props. Many species of Lentinus also under such conditions form, instead of the 'stalked' pileus, white cylindric strands which remain either simple or make coral-like branchings. If such branches reach the light, they commonly produce at the apex reduced or more or less normal pilei. Here then the influence of the light favours the formation of the pileus; it does not affect the first primordia of the fructification. Similarly in some species of Coprinus, for instance, C. stercorarius, C. plicatilis, C. ephemerus, isolated primordia of fructifications appear in the dark, but they do not unfold normally, the cap is arrested while the stipe is abnormally elongated; in light, on the other hand, the fructifications are very freely laid down almost to the complete

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[1] Woronin in De Bary and Woronin, Beitr. zur Morphologie und Physiologie der Pilze, iii. p. 10.

[2] St. Schulzer v. Müggenburg, Des Allbelebenden Lichtes Einfluss auf die Pilzwelt, in Flora, 1878, p. 118. Older observations, including those of Fries, are cited by Elfving, Studien über die Einwirkung des Lichtes auf Pilze, Helsingfors, 1890.

[3] See Brefeld, Untersuchungen aus dem Gesammtgebiete der Mykologie, iii. pp. 87, 114, 115; viii. p. 275; also Schröter, Über das Wachstum der Pilze im Dunkeln, in Jahresber. der Schlesisch. Gesellsch., 1884, p. 290.

exhaustion of the mycelium. Other species of Coprinus remain quite sterile in darkness, for instance, C. niveus, C. nycthemerus. The primordium of the fructification is directly dependent upon light, and especially upon the more highly refrangible rays. Once the primordia have been laid down under the influence of light and have reached a certain stage of development, the ripening and unfolding can go on in the darkness, just as is the case with flowers, whilst the still small primordia of fructifications dwindle coincidently with the elongation of their stipe. Light must then act here up to a certain stage of development; if this be the case, then the process of ripening may take place in the darkness. It is remarkable that in Coprinus stercorarius the formation of the pileus is not suppressed, as is usual, in darkness if the temperature be high, or at least it is only partially suppressed, and complete pilei may be formed, although much more slowly than they are in the presence of light.

C. Influence of the Medium.

We have in this chapter to consider all those conditions of the plant which are brought about by the state of aggregation, or the chemical composition of the surroundings or 'medium' in which it grows. We leave out of view then purely quantitative differences as well as the deviations which can be designated 'malformations'[1]; we also pass over among other things the phenomena of dwarfing or 'nanismus,' especially as the deviations that appear in dwarf-forms and which are usually the result of an insufficient water-supply require further investigation in their relation to normal forms. When Frank[2], for example, says: 'Leaf-form may also essentially change, thus dwarf Capsella Bursa-pastoris and Teesdalia nudicaulis may occur with simple entire instead of pinnate leaves,'—we learn nothing about the behaviour of the dwarf from such a statement. In the first place the primary leaves in Capsella are always undivided, and the dwarf might have remained in the stage of primary leaves, and in the second place the form of the leaves in Capsella is a fluctuating one, therefore one must, in order to get accurate results, compare the leaf-formation in dwarf plants and normal plants which are *sister*-plants. The changes of form which are brought about by such mechanical influences as pressure do not fall to be considered here.

[1] These have been spoken of in the Fourth Section. See p. 177.

[2] Frank, Die Krankheiten der Pflanzen, 2. Aufl. p. 274.

1. INFLUENCE OF WATER AND AIR-MOISTURE.

A. AQUATIC AND AMPHIBIOUS PLANTS [1].

In aquatic plants the submerged leaves have frequently a different conformation from those which stand above the surface of the water or float upon it, and there are two forms which are specially characteristic [2]—the riband-form like that of many monocotyledonous plants, and the greatly divided form which occurs in many dicotyledonous plants. Similarly, plants which have the capacity to form two kinds of shoots —those which are adapted to a water-life, and those which are adapted to a land-life—commonly produce leaves of different form on the different shoots. Superficial observation would lead us to the view that the peculiar form of the water-leaves must be ascribed to a *direct* influence of the medium. But it is only in relatively few cases that we can prove this, and of course we cannot exclude the probability that in the other cases we have to deal with an inherited adaptation. Besides, it must be remembered that a submerged plant is in conditions of illumination, of temperature, and of nutrition, very different from those of land-plants, and, as has been pointed out in the section upon the influence of light, we know that by feeble illumination Sagittaria may be reduced again to the condition in which it forms the 'riband-shaped leaf' typical of the water-leaves under the normal conditions. We have further seen [3] that Sagittaria natans can be caused to revert to the formation of riband-like juvenile leaves by the influence of different factors quite independently of the 'medium.'

In species of Jussiaea, a direct influence of the medium can be traced [4]. The peculiar spongy breathing roots of Jussiaea grandiflora do not appear if the plant grows upon dry soil. The same may be said of the 'knee-roots' of Taxodium distichum.

The configuration and anatomical structure of the leaves of many amphibious plants are quite different according as the plant grows in water or on land. Thus the water-leaves of Ranunculus fluitans are radially constructed, those of the land-form are altogether different and possess dorsiventral lobes [5]. We must consider the latter leaf-form as the more primitive; it conforms essentially with those of the land-species of Ranunculus. It is also easy to establish in other amphibious species of Ranunculus that the leaves of the water-form have finer and longer lobes than those of the land-form, although the differences

[1] The formation of organs in these plants will be found fully described in my 'Pflanzenbiologische Schilderungen,' ii.; I give therefore here only a short summary.

[2] See the Third Section, p. 164.

[3] See p. 172.

[4] See the figures in my 'Pflanzenbiologische Schilderungen,' ii.

[5] Goebel, Pflanzenbiologische Schilderungen, ii. figs. 97 and 98.

are not so great as appear in R. fluitans, which is one of the species whose adaptation is chiefly to an aquatic life. Ranunculus multifidus, which stands very near the land-species of the genus, illustrates a direct influence upon leaf-form—its submerged leaves are much more finely divided than the usual land-leaves (Fig. 128), and show in that way an approach to the behaviour of the characteristically water-species [1].

In many of the Bryophyta moisture plays a part in the formation of organs. Frullania dilatata possesses cap-like formations formed by invaginations of leaf-lobes which serve the plant, living as it does upon the bark of trees, as capillary water-reservoirs. Their formation can be hindered by continuous culture in moisture; then the leaf-lobes remain flat [2]. Bryum argentum owes its silvery sheen to the death of the upper portions of the leaves which, as a non-living envelope, protect the buds against great drought; if the plant be cultivated in moisture the leaves remain green [3]. Likewise in many mosses we find that the hair-points on their leaves, which are present in plants growing upon dry sunny spots, and which there serve as protecting tufts to the stem-buds, are not developed when the plants are grown in moist places or in water.

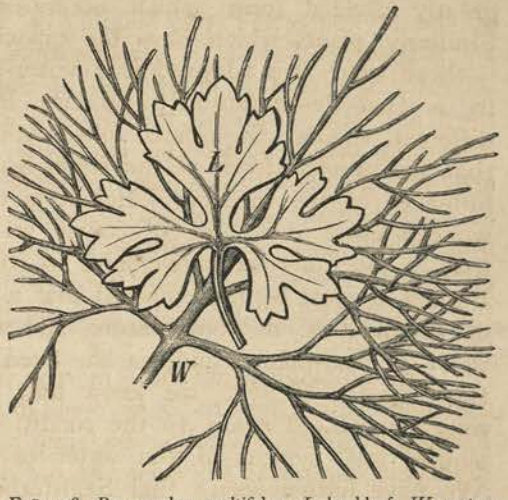

FIG. 128. Ranunculus multifidus. *L*, land-leaf. *W*, water-leaf.

B. THE INDUCTION OF RESTING STATES THROUGH DROUGHT.

In some Thallophyta drought causes the formation of resting states the appearance of which is often associated with a profound change in the whole formation of organs. Thus in Botrydium granulatum [4], one of the Siphonieae, which consists of a bladder-like green upper portion and a branched root-like subterranean portion, if it is subjected to drought or strong insolation, the protoplasm wanders into the rooting portion and breaks up into a number of cells which, under

[1] Regarding the complex relationship of Ranunculus aquatilis, see Goebel, Pflanzenbiologische Schilderungen, ii. p. 309.

[2] Goebel, Pflanzenbiologische Schilderungen, i. fig. 76.

[3] See Flora, 1896, p. 10.

[4] See Rostafinski und Woronin, Über Botrydium granulatum, in Botan. Zeitung 1877, 649.

favourable circumstances, may again develop further, whilst the emptied upper portion dies away. Vaucheria geminata[1] behaves in quite the same way, only the breaking up into single cells takes place within the green tube of the plant; it divides into a number of thick-walled cysts which protect the protoplasm better against drought than would be the case were the threads merely to pass over into a resting condition without becoming divided.

This construction corresponds with the formation of the sclerotium of the Myxomycetes, the building of which is likewise associated with an important change in configuration of the vegetative body. These sclerotia are resting conditions of the mature plasmodia[2], and when they are being formed the delicate processes of the plasmodium are drawn in and it breaks up into cells, invested by a membrane, which are capable of withstanding drought. This resting condition appears as a consequence of prolonged drought, but it seems also to be a consequence of unfavourable nutrition as well as of other unfavourable influences. A similar resting condition from similar causes may be assumed by the swarm-cells or amoebae and the juvenile plasmodia; they become thick-walled cysts.

The protonema of some mosses has the same capacity and under unfavourable circumstances becomes divided into isolated cells. Thus in Funaria hygrometrica colourless 'limiting' cells whose walls become partly mucilaginous appear between the ordinary green protoplasmic cells and bring about a separation of these cells which remain alive[3]. The biological significance of these processes is chiefly to be found in the fact that the isolated cells can more easily again attain to favourable conditions.

In the higher plants the appearance of resting conditions, which correspond biologically with those of the plasmodia, are in most cases independent of external influences, in gardening practice however an earlier commencement of the resting period is brought about by a slackening of the water-supply in plants which are destined to be 'forced.'

C. FORMATION OF TUBERS IN JUNCUS AND IN POA BULBOSA.

The formation of tubers in Juncus supinus and other species requires further experimental and anatomical examination. According

[1] Stahl, Über die Ruhezustände der Vaucheria geminata, in Botan. Zeitung, 1879, p. 129. In Oedocladium protonema, referred to in the text on p. 256, resting stages arise which are able to resist long desiccation, but such states also develop on the subterranean parts of plants growing normally; see Stahl in Pringsh. Jahrb. xxiii. p. 343.

[2] See de Bary, Die Mycetozoen, p. 460; Cienkowski, Das Plasmodium, in Pringsh. Jahrb. iii. p. 422.

[3] Goebel, Die Muscineen, p. 389; Id. Über Jugendformen von Pflanzen und deren künstliche wiederhervorrufung, in Sitzungsber. der. k. bayer. Akad. d. Wissensch. xxvi (1896), p. 456.

to Buchenau[1] it is dependent upon habitat. It is suppressed on plants which grow on persistently wet places, but occurs on the other hand frequently on those which grow on warm sandy places. We do not however yet know what part these tubers play in the plant-economy, whether they are intended to store water, or are simply a consequence of an arrest of growth in length. Poa bulbosa appears to behave quite like those species of Juncus.

D. FORMATION OF THORNS AND PRICKLES.

Lothelier[2] has recently published a number of statements regarding the influence of air, moisture, and illumination upon the formation of organs in plants provided with thorns and spikes, and if these are correct they have a considerable interest; but they require confirmation, and I, at least, have not yet succeeded in proving the striking effects enunciated by Lothelier. What he maintains is, that thorns, whether they be branch-thorns, as in Ulex, or leaf-thorns, have the 'tendency' to assume the form of normal twigs or leaves when the plants are grown in an atmosphere saturated with moisture, in other words, the thorn-formation is suppressed, whilst in Robinia the thorns disappear in these conditions. Plants cultivated in moist air are in their anatomical relationships less differentiated, especially in the matter of their sclerenchymatous tissue, and this is known from other investigations. These anatomical relationships, however, do not come into consideration here. It is of course well known that plants provided with thorns and prickles are specially numerous in dry areas; the floras of desert and steppe regions furnish abundant examples. This may be a consequence of either a direct adaptation to the dry climate, or the survival of such forms as were protected against animals. On the other hand in the North Arctic region, which is characterized by poverty in plant-eating animals, other xerophilous adaptations occur, rolled-leaves and others, but, so far as I know, never prickles or thorns. We may find naturally different grounds for this want: the small number of arctic plants makes the existence of forms which would produce thorns under the influence of the environment less probable; the shortness of the period of vegetation would favour such plants as did not make use of their assimilation-capacity for the formation of organs useless in the existing conditions, and so on. Among the inhabitants of the dry regions of the high Andes also we do not find, apart from the

[1] Buchenau, Über Knollen-und Zwiebelbildung bei den Juncaceen, in Flora, 1891, p. 75.

[2] Lothelier, Influence de l'état hygrométrique et de l'éclairement sur les tiges et les feuilles des plantes à piquants, Lille, 1893; also in Revue générale de Botanique, v. p. 480.

Cacteae, many prickly or thorny plants, although there are some, such as species of Nassovia. A dry climate with strong insolation has always been considered favourable to the formation of thorns, but this assuredly cannot be the only factor, for the long prickles which appear upon the under surface of the floating leaves of Victoria regia, and to a smaller degree in Euryale ferox, could not have arisen through the influence of drought. What is really wanted here is experimental evidence, of which we have none, except that of Lothelier. I have never been able to prevent the formation of thorns in plants of Ulex which I kept for ever so long under bell-jars in a saturated atmosphere; the shoots, developing into thorns, became in moist air longer, and developed their leaves more, but there was no retarding of the formation of thorns in my experiment. Lothelier figures the apex of the plant which produced leafy shoots instead of thorns, but if he had cultivated the plant longer[1] the apparent leafy shoots might have become thorns. Lothelier's statements give me the impression that he has selected single cases specially favourable to his interpretation, without having undertaken a careful testing of the whole of the experimental cultivation. In other words, I do not think that up till now any more has been proved than that in moist air the formation of prickles and thorns is *retarded*, there is not proof that it can be *suppressed*. That the formation of thorns and prickles is dependent on quite definite factors is shown by the case of Ilex Aquifolium, where prickles appear only on the leaves of young plants, not on the leaves of the older ones. One might bring this into conformity with the fact that in older plants, in consequence of the stronger development of the root-system, the nutrition, especially the water-supply, is better, and this would then be a case similar to that of many other plants, in which it has been established that they lose their thorns in good soil.

E. SUCCULENCE OF THE LEAF.

Whilst it has not yet been established with certainty that other relationships of configuration are directly dependent upon water-supply or transpiration, it is possible that the succulence of the leaves of many plants which grow in localities deficient in water may be considered as belonging to this category. Such succulent leaves serving for water-storage diverge usually in their form from ordinary leaves, and it is possible, though

[1] In plants of Crataegus pyracantha grown in moist air, Lothelier found the lowermost twigs only ended in a thorn, 'all the others, having been subjected for a longer time to the influence of the medium, were terminated by tufts of leaves at the period when the plant was cut.' I will only say two things regarding this: (1) many lateral shoots of the higher order developed, as is shown in the drawing, even in darkness into thorns; (2) the lateral shoots of the first order had not grown out 'at the period when the plant was cut.'

not proved, that this divergence is caused in many plants directly by environment.

Thus Johow[1] states regarding Philoxerus vermiculatus, a West Indian shore-plant of the family of Amarantaceae, that the leaves possess in sunny spots a cylindric form, whilst in the shade, where the plant sometimes, though exceptionally, develops, they are generally thin and disk-like. As I have already pointed out[2], the causes for the change of form here are altogether indistinct, inasmuch as the substratum according as it has a greater or a less amount of salt, as well as the different conditions of transpiration in sun and shade, might be considered as having effect as well as the direct insolation.

Battandier[3] points out that some Algerian species of Sedum which grow in moist spots, for instance, S. stellatum and S. tuberosum, have flat leaves, while species like S. rubens and S. Magnolii, which grow on dry spots, have in the moist period of the year flat leaves, in the dry season cylindric leaves, and that in S. Clusianum the leaves in cultivation have a 'tendency' to become flat. These observations however only show us that the configuration of the leaf stands in relation to the environment, but they do not tell us whether environment *directly* acts upon them. Most of our woody plants form at the end of their period of vegetation leaves different from those they produced at its commencement, that is to say, scale-leaves, but the difference is not directly caused by external factors. How the species of Sedum just mentioned behave can only be ascertained after exact experimental cultivation.

2. HALOPHILOUS PLANTS.

The majority of the higher plants are unable to grow in a soil which contains more than 0·02 per cent. of chloride of sodium. The vegetation of the seashore or of salt marshes is therefore relatively poor in species. Of plants which are able to grow in such places the majority are distinguished by peculiarities of form which occur otherwise in the inhabitants of dry areas—such for example as succulence of the leaves or shoots, reduction of the leaves, as in species of Salicornia, and other features which impede transpiration[4]. These features are primarily connected with the fact that the absorption of water from the soil is made difficult by the presence of salt, and that water evaporates with greater difficulty

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[1] Johow, in Pringsh. Jahrb. xv. p. 305.

[2] Goebel, Pflanzenbiologische Schilderungen, i. p. 31.

[3] Battandier, Quelques mots sur les causes de la localisation des espèces d'une région, in Bull. de la Soc. Bot. de France, 1887, p. 189.

[4] See the description of the peculiar leaf-construction in Acantholippia and Niederleinia in my 'Pflanzenbiologische Schilderungen,' ii. p. 13.

from cells rich in salt than from cells which do not contain so much[1]. We see consequently that many plants which become flooded with salt water place their leaves in the profile position, like plants subjected to strong insolation, in order to provide a protection against too strong evaporation. Here, however, the question is how far the relationships of configuration of the halophytes are *directly* caused by the life-relationships. As in other groups, we find amongst them plants whose configuration is fixed, and even under diverging conditions is not changed, at least not in the first generation; and again there are plants in which such a change does take place. Thus many plants, like Lotus corniculatus, Plantago major, Atriplex rosea, Blitum polymorphum, Scrophularia frutescens, produce on the shore more fleshy leaves than they do when grown inland, whilst the leaves of Salsola Kali, Halogeton sativus, and others, are thinner when the plants are growing upon a soil without salt, than is usual on plants growing on saline ground.

Lesage[2] has carried out a series of experimental cultivations which show that in some plants, Lepidium sativum, for example, the succulence of the leaf depends upon the possession of salt; when this condition exists the palisade-cells are especially strongly developed, the intercellular spaces are less conspicuous, the chlorophyll-corpuscles are not numerous, and the whole plant remains stunted.

3. FUNGI.

The influence of nutrition upon many fungi is most characteristic. Several of the facts bearing upon this subject have already been mentioned in the chapter upon malformations, here we have only to do with effects upon the 'normal' sequence of development from which of course the abnormal is not sharply separated.

If the zygospore of Mucor, richly filled with reserve-material, be allowed to germinate in the air, it forms no mycelium but a germ-tube which ends with a sporangium (Fig. 129); but if germination takes place in fluid, a mycelium arises, upon which numerous sporangia subsequently appear. The formation of these sporangia however can take place only in the air, not in a fluid, according to Brefeld. The 'gemmae,' which are cells rich in contents, developed under definite

[1] Stahl, Einige Versuche über Transpiration und Assimilation, in Botan. Zeitung, 1894, p. 117. Stahl found that in plants which are not 'halophilous' the stomata are closed by the absorption of common salt, and he concludes that this is why our ordinary plants do not appear upon the seashore. I believe however that there is something more operative here and that the salt itself has a direct harmful influence. Most submerged Spermaphyta do not thrive in water which is even slightly salt. The fact that the stomata remain open in halophytes seems to me to indicate only their want of the usual mechanism for regulating transpiration.

[2] Lesage, Recherches expérimentales sur les modifications des feuilles chez les plantes maritimes, in Revue générale de Botanique, ii (1890).

circumstances on the mycelium of Mucor racemosus[1], behave in quite the same way; the formation of sporangia takes place here only in the air, in a fluid the gemmae form mycelia. If Mucor racemosus grows in a nourishing solution of some depth rich in sugar, its mycelium forms septa and a series of cells rich in plasm is developed. If the depth of the solution be shallow, and the solution itself dilute, phenomena like those which are the result of bad nutrition appear—the protoplasm of the mycelium aggregates and becomes so divided by septa that a series of

FIG. 129. Mucor Mucedo. Stages in the formation and germination of the zygospore. 1, mycelial branches conjugating. 2, abjunction of the conjugating cells *a a* from the suspensors *b b*. 3, conjugating cells more evident, warts on the membrane beginning to form. 4, ripe zygospore *b* between the suspensors *a*. 5, sporophore arising directly from the zygospore. After Brefeld. 1-4 magn. 225; 5 magn. about 60. Lehrb.

FIG. 130. Ampelopsis. Tendrils, *R*, with anchoring disks at the ends of the branches. Lehrb.

chambers alternately rich in protoplasm and empty of protoplasm are produced—a process recalling the formation of isolated cells by the protonema of many mosses[2].

The mycelium of Mucor racemosus, but not that of Mucor Mucedo, can on the other hand pass over into the sprouting form. This happens if

[1] Brefeld, Untersuchungen aus dem Gesammtgebiete der Mykologie, viii. p. 212; Klebs, Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen, p. 496. To the latter work I refer for an exhaustive account of the conditions determining the appearance of mycelium and sporophore.

[2] See p. 262.

the spores are sown in a solution of less nutrient value, especially if they are submerged in a fermentable sugar-solution, and are restricted in their supply of air. There appears then a copious formation of cross-walls, and the single cells which thus arise increase by sprouting. Similar processes are found in some other forms, but we cannot further discuss the subject [1].

D. Mechanical Stimuli [2].

Mohl was the first to show that the adhesive disks on the tendrils of certain species of Ampelopsis appear in consequence of contact with a firm body (Fig. 130). We have here to do with a contact-stimulus. Different species of Ampelopsis behave differently. Some, like A. hederacea, possess ordinary tendrils which twine round a support and eventually become firm woody structures, but if they do not happen to find a support they die off at an early period. Ampelopsis quinquefolia, on the other hand, fixes itself to walls and tree-trunks, by means of adhesive disks on its tendrils [3], but these can also act like ordinary tendrils. In tendrils which do not come into contact with a firm body, no viscid disks appear; the primordia of these are nevertheless so far apparent in that the epidermal cells of the convex side of the tip of the tendril are elongated in a radial direction—a condition which does not occur in the tendrils of other species of Ampelopsis. By the strong elongation and the periclinal division of these after the contact-stimulus has been applied, as well as by an elongation in radial direction of the cells lying immediately beneath the epidermis, the formation of the adhesive disk is brought about. The adhesion is caused by the disk adjusting itself to all the inequalities of the surface of the substratum and secreting a sticky substance [4]. It is interesting to note that in Ampelopis Veitchii the formation of the adhesive disks has proceeded a considerable stage before a contact-stimulus can operate; the primordia of the disks are visible as small swellings on the tips of the tendrils, but their further development into adhesive organs is dependent upon a contact-stimulus.

The tendrils of some Bignoniaceae, for instance, Bignonia littoralis, B. capreolata, Hanburya mexicana, and according to Naudin [5] those also of the cucurbitaceous Peponopsis adhaerens, form in like manner adhesive disks in consequence of contact-stimuli. It is worthy of note that the trifid tendrils of the bignoniaceous genus Haplolophium end in smooth shining adhesive disks before contact with the support; when they adhere they sometimes become very broad [6]. Von Mohl first showed that the haustoria of Cuscuta arise in consequence of a contact-stimulus which can induce their formation on all sides of the shoot-axis [7].

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[1] See Zopf, Die Pilze, p. 271, in Schenk's Handbuch der Botanik, iv.

[2] A comprehensive discussion of this subject falls more within the sphere of Physiology than of Morphology; but I cannot altogether pass it over here.

[3] See the figure in Sachs, Lectures on the Physiology of Plants, p. 667.

[4] See A. von Lengerken, Die Bildung der Haftballen an den Ranken einiger Arten der Gattung Ampelopsis, in Botan. Zeitung, 1885.

[5] Naudin, in Ann. d. Sciences Nat. sér. 4, xii (1859), p. 89.

[6] Fritz Müller, Notes on some climbing plants near Desterro, in Journ. Linn. Soc., ix. p. 348.

[7] See also Peirce, A contribution to the physiology of the genus Cuscuta, in Annals of Botany, viii.

Analogous cases occur amongst the lower plants. Riccia fluitans exhibits a land-form and a water-form. The former has numerous hair-roots, the latter has usually none; but if the water-form be allowed to swim upon a fine sieve it also produces the hair-roots, and it is evident their usual suppression upon it is due to the want of a contact-stimulus in the water [1].

We can say the same of the Fungi. The mycelial threads [2] of Peziza tuberosa and P. sclerotiorum [3] form tufts of hyphae in consequence of contact, and these serve as anchoring organs; similarly Mucor stolonifer [4] produces rhizoids on its stolons. Büsgen [5] found in different parasitic fungi that they only produced anchoring organs when they touched some firm body; the formation of haustoria, on the other hand, was usually the result of a chemical stimulus [6].

Borge [7] has investigated the formation of anchoring organs in some Chlorophyceae amongst the Algae. The species of the genus Spirogyra exhibit very different behaviour. Some have the capacity to form rhizoids under special external conditions, others do not possess this power. To the former belongs Spirogyra fluviatilis, which can grow fixed upon stones in flowing water. The rhizoids which act as its anchoring organs arise in consequence of contact, but other conditions may induce their formation, for example, cultivation in a solution of cane-sugar or of urea of a certain concentration [8]. It is noteworthy that all the cells of the filament, which has not a polar construction, possess the capacity to form rhizoids, but the cells forming them must be terminal cells, or at least lie in the neighbourhood of a terminal cell. Should dead cells occur in the middle of a filament, the adjacent living cells are to be considered as terminal cells. In Vaucheria clavata the capacity to form rhizoids is limited to the germ-plants, and is stimulated to activity in these by contact. If these rhizoids be cut off, the wound heals, and then long threads grow out which, notwithstanding contact, do not form rhizoids, but in other filamentous Algae, for example, species of Cladophora, Draparnaldia glomerata, rhizoids may arise without contact, and if these be cut off new ones can be developed to take their place. The adhesive disks of Plocamium (Fig. 45) doubtless arise in consequence of contact, and they behave quite like those of Ampelopsis.

It is difficult to determine whether we have to do with mechanical or with chemical stimuli in the fertilization-processes which we observe in the flowers of dicotyledonous and monocotyledonous plants; it is most probable they are chemical. At the time of pollination in such plants as Corylus, Alnus Quercus, and their allies, there is no sign of the placenta in the ovary, far less of the ovules, and in the Orchideae the ovules in most species are indeed laid down at the time of pollination, but are still

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[1] Regarding Marchantia, see Pfeffer in Arb. d. bot. Instituts in Würzburg, i. p. 77.

[2] Brefeld, Untersuchungen a. d. Gesammtgebiete d. Mykologie, iv. p. 112.

[3] De Bary, in Botan. Zeitung, 1886, p. 382.

[4] Wortmann, in Botan. Zeitung, 1881, p. 385.

[5] Büsgen, Über einige Eigenschaften der Keimlinge parasitischer Pilze, in Botan. Zeitung, 1893, p. 53. The literature is cited here.

[6] See also Miyoshi, in Botan. Zeitung, 1894, p. 1; Id. Pringsh. Jahrb. xxviii.

[7] Borge, Über die Rhizoidenbildung bei einigen fadenförmigen Chlorophyceen, Upsala, 1894.

[8] 0·5–0·25 per cent. in the case of cane-sugar, 0·4–0·2 per cent. in the case of urea.

rudimentary; the stimulus exercised by the pollen-tube induces the further development of the female sexual apparatus in these plants. That this stimulus has nothing to do with the fertilizing influence of the pollen-tube is in the nature of the case evident, and moreover it is exercised by foreign pollen in orchids which are incapable of hybridization.

The following observation of Treub[1] is of particular interest:—Individuals of Liparis latifolia have been found on which the ovary of closed flower-buds was swollen up, and contained ovules just like those which would otherwise develop only after pollination. No pollination had been effected, but the ovaries were infested by small insect-larvae which had brought about the same effect as usually follows the action of the pollen-tube. The pollen-tube in its growth abstracts from the style and the ovary the material necessary for its elongation and therefore determines a flow of plastic material to the ovary. The larvae had exactly the same influence. Of similar nature, only less striking, is the well-known fact that apples and pears which are inhabited by larvae ripen earlier than do others. The very varied processes which are observed in the ripening of fructifications of lower and higher plants evidently belong to the same category.

[1] Treub, L'action des tubes polliniques sur le développement des ovules chez les Orchidées, in Ann. du Jardin botanique de Buitenzorg, iii. p. 122.

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